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THE LOCOMOTION OF FISHES[1]

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INTRODUCTION

(Figs. 39–83 incl.)

The locomotion of animal forms has been studied in more or less detail from time immemorial, certain ancient mechanical devices, such as the oar, battering ram, et cetera, having been obviously based on the observation of the performances of organic structures. In historic times biologists, physicists and engineers have investigated the problem of animal locomotion from both the philosophical and the utilitarian standpoints, striving for various reasons to attain a better understanding of the physical laws underlying the multiform locomotor efforts of the various animate objects moving about them. Many of these laws, when understood, have been applied to useful mechanical devices. Frequently the methods of the animals studied have been surpassed, for in many cases it has been possible to go beyond the limitations of animal structure in the employment of the inert materials used in machine construction. The manifold significance to biologists of the manner in which changes in position are effected by animals from the osteological, myological, phylogenetic and the purely philosophical standpoints are too patent to require elaboration.

In spite of the large amount of work done, there still remain many poorly understood, and even some misunderstood, methods of producing changes in spatial relationships that have even been employed by animals existing long before the advent of man. Progress through the water as exemplified by fishes is prominent among those methods that are comparatively slightly understood even though phases of it appeared early in geologic history. The problem is complicated, as is any study involving observations on living fishes, by the fact that the subjects inhabit a different medium

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[1] Awarded the A. Cressy Morrison Prize in 1925, by the New York Academy of Sciences.

than that which is necessary for the life of the observer. Further, they often fail to act in a normal manner when confined in a glass-sided vessel, and in a considerable number of cases it is even impossible to successfully transfer them to such a container in a healthy state.

The accompanying bibliography testifies to the widespread interest this field of study has stimulated, although it is surprising to note that so much of the work has been in the nature of abstract philosophical discussion and that relatively so little has been based upon actual experiment and study of living fishes. While there is an extensive literature on the locomotion of fishes, as just noted, much has been left unanalyzed and unexplained. It is the purpose of the present paper, therefore, to amplify our existing incomplete knowledge of the subject as much as possible at this time; to refute that which is untrue in its literature, and finally to unify and systematize the whole. The hope is entertained that it will be of use to both the philosophical biologist and the practical student who may seek in natural phenomena an inspiration for his inventive genius.

In developing the present paper the author has carefully confined himself to a consideration of the physical forces and the external body forms involved in the movements of fishes. All anatomical details concerning the manner in which a given movement is accomplished have been avoided as much as possible, as it is felt that such details might better be the subject of a separate dissertation. Thus for the present purposes, fishes are simply considered as mechanisms capable of reacting to their environment in various ways, so as to effect their spatial relationships. How their acts produce the known results is the only question under consideration. It is evident that such data are a prerequisite to a thoroughly satisfactory explanation of the various types of locomotor organization among fishes.

It was found advisable to consult a considerable number of people concerning the various points herein discussed. The points of view so obtained varied greatly and as a consequence much profit was derived in the way of suggestions, corrections and criticisms. To these gentlemen who gave generously of their thoughts and time the author is greatly indebted, and is especially beholden to Prof. W. K. Gregory, of Columbia University and the American

Museum of Natural History, for advice and general encouragement; to Mr. J. T. Nichols, for translating certain papers and for philosophic criticism, to Dr. E. W. Gudger, for bibliographic aid, both of the American Museum; to Dr. C. H. Townsend, of the New York Aquarium, for various facilities; and to Mr. L. L. Mowbray, also of the Aquarium, for descriptions of the behavior of certain fishes afield not seen personally; to Dr. G. B. Pegram, Dean of the Department of Physics Columbia University; Mr. C. M. Paxton, inventor, Mr. E. C. Bennett, naval architect, and the Blakeman-Hartshorn Co., consulting engineers, for mechanical and mathematical data; to Mr. Will Simmons, artist and student of animal life, and to his father, for criticism and editorial assistance.

The paper has been divided into two chief parts: "Part I—Physical," which treats of the locomotor efforts of fishes, grouped according to various characteristic types of movement, and "Part II—Systematic," which treats of the way in which typical representatives of the larger taxonomic groups use their locomotor apparatus.

Following these are the conclusions drawn, and various information of an appended nature.

The various divisions and subdivisions are indicated in the Outline below. As such a subject is naturally intricate, many cross-references have been inserted, for nearly every part bears in some way on every other.

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PART I—PHYSICAL

INTRODUCTION

Although the term "fishes" is used to designate an extremely diversified assemblage of vertebrates, there is, nevertheless, a basic similarity in all their multiform movements, for with the exception of a few highly specialized off-shoots, they retain a primitive metameral arrangement of the lateral body muscles such as is not found in the tetrapods. The paired appendages are not ordinarily controlled by such huge muscle masses as in the tetrapods, in which the conditions are reversed, for there the emphasis is commonly placed on the paired limbs. Thus all the fishes may be considered under one rather natural locomotor grouping.

On account of the density of water, it is necessary that an extremely fine streamline form be attained if any considerable speed is requisite. This fact at once limits fishes requiring considerable mobility to a symmetrical, evenly rounded, unangulated and somewhat fusiform outline. With such a form, made necessary by evident mechanical circumstances, the primitive metamerism, together with other generally varying though often restricted features, gives ample means for the production of all necessary speed and agility. In forms that have departed radically from the basic bio-physical necessity of a streamline form, a decided restriction of speed is at once apparent, which is proportional to the amount of departure from the typical ichthyized form. In fact, only where mobility ceases to be important can these frequently bizarre forms, survive.

Tetrapods that have returned to an aquatic habitat, such as Cetaceans and the extinct Ichthyosaurs, have revived the old streamline forms wherever speed was necessary. The musculature, while differing in detail on account of widely different ancestry, has revived the old body movements, especially in those with elongate fish-like bodies, the only ones that have acquired speed in swimming.[2]

The average vertebrate animal, excluding the heavily armored ones, has a specific gravity approximating that of sea water, if the buoyant effect of the lung cavity in pulmonate forms be discounted. This may be associated with a remote ancestry adapted to an aquatic existence. Fishes, at least, seem to have been able to approximate closely the various specific gravities of the different densities in which they are found without any profound specialization. This has been done principally by means of the air bladder, which effects a great muscular economy entirely unknown to terrestrial animals which leave *terra firma* in locomotor flight. It is clear that for insects or birds to develop a sufficiently large sack for containing some substance lighter than air, they would require an immense and unwieldy apparatus for lifting their bulk in such a tenuous medium. Gliding animals, such as flying squirrels, are, of course, out of the discussion as are the ballooning spiders which simply drift about with air currents. The latter are more comparable to planctonic forms with extended surfaces to assist in flotation. In this connection a typical fish might better be likened to a dirigible

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[2] The body movements may even be in another plane as seen commonly in the cetaceans.

balloon than to any truly flying animal, which is fundamentally more nearly similar to an aeroplane.

On account of the much greater density of water, the reaction of forces through or in it is much more direct than in such a tenuous medium as air. Therefore in comparisons of apparently similar creatures inhabiting either sphere respectively, due allowance must be made for this difference. It might be said that movement in water is slowed as compared with that in air, as every swimmer knows. A submarine motion picture bears a considerable resemblance to a slowed study of a certain speed. This simply means that a much greater resistance is encountered in water than in air, and that in the interest of economy a much closer approach must be made to the ideal streamline form. Partly offsetting this is the greater reactance of any stroke under water, which is also due to its density. In water, certain differentials may become reversed. For example, in forms with a specific gravity of less than that of their habitat, the inverse of gravitational effect is felt, proportional to the difference in the two specific gravities. However, in most fishes the specific gravity is so nearly that of their native waters that the effect is practically nil.

In a study of the motor efforts of fishes the following factors and conditions are always to be kept in mind. For a reaction to be possible, it must conform to these conditions:

1. A given set of motional phenomena must be attributed to an appropriate set of forces applied by the fish to the water and the resulting reaction of the water on the fish.
2. To produce the appropriate set of forces the fish in question must be physically able to move the various members in a manner that the occasion demands.
3. The fish must be observed to actually perform in the given manner

Obvious as these three statements are, it seems necessary to give them, as there exist, in the literature of the subject, numerous instances where students have boldly neglected such considerations.

As it is possible that the same result may be obtained in any one of several ways, it takes no little patience to observe clearly and note the motions of the various elements involved, and to resolve the resultant into its often numerous components. In this connection the study of motion picture film prints and numerous still pictures has proved invaluable.

For purposes of convenience the present section is first divided under three main heading groups as follows: (1) Forward Rectilinear Movement, (2) Maneuvering, and (3) Movements Other Than Swimming, such as creeping, leaping and flying. The first two topics include not only movements commonly referred to as swimming but also all other acts of special adjustment on the part of a fish that is free from any contact with solid surfaces. To simplify matters, in all cases except where mention is made to the contrary, it is understood that the fish studied is in perfectly still water, because, unless some special use is made of a current, a fish is either carried along with it, the actual course being the resultant of the current and of the fish's own direction of motion, or some special act is performed to offset the effect of the current. Following these sections are two more special ones: (4) "Reomorphism," which deals in a general way with the external form of fishes, and (5) "Relations to habits and development," which considers briefly the influence of these factors on locomotion.

FORWARD RECTILINEAR MOVEMENT.

Under this heading are considered all basic methods employed to produce a straight forward horizontal motion in still water while free from contact with any solid. This section covers those movements here referred to as swimming (in the restricted sense).

Body Movements.

Nearly all fishes make some use of flexures of the trunk and tail portions of the body for the purpose of inducing forward progression. In only a few aberrant forms is this not done, for even most fishes that use the fins as the chief locomotor organs, will, at times of extreme hurry, resort to this more primitive method as an auxiliary, if their bodies are not so highly specialized as to prevent it. What at first appear to be two distinct types of oscillation are mechanically possible in the bodies of fishes in which a muscular metamerism is persistent. These are : (1) a somewhat serpentine motion as seen in the waving of a flag; which is induced by differential alternate contractions of the myomeres and is subsequently referred to as the *anguilliform* motion; (2) a wig-wag motion somewhat as seen in a fan, which is induced by a nearly simultaneous contraction of all the myomeres on each side, alternately, this is subsequently referred to as *ostraciiform*. These two movements are not as distinct as would first appear and are usually seen as elements of a single motion. It is only in the extremes that one stands out clearly through the lessened complication of the other. With this thought in mind these two motions may be described and analyzed separately as follows:

Anguilliform Movement: One extreme type may be so termed for it is illustrated almost perfectly in the Anguillidae and similar long-bodied forms. Primarily, this type of movement consists in throwing the anterior portion of the body into what is practically a sine curve and in passing this curve backwards by differential alternate contractions and relaxations of the serial myomeres. A mechanically analogous movement may be effected by grasping a long rope at one end and giving it a quick jerk at right angles to its axis. A wave will be seen to pass down it, dying out eventually because the one action alone is the impelling agent, whereas in the case of the living body an added impetus is imparted by each successive myomere. As soon as the first wave is completely formed and started rearward, a second follows, but on the opposite side, and so on alternately, giving the animal its typical waving motion. The initial wave is started by contracting the first few myomeres on one side of the body in such a manner as to slightly flex the head and to a less degree the posterior part of the body and form the first curve, or the wave may start further back, leaving the head practically still. The wave is then carried back by contracting the next posterior myomere and relaxing the first contracted one progressively.

Maurey (1895) in studying animal locomotion in general, published two illustrations of a swimming eel which show this character of the anguilliform movement admirably, although he made no mention of the forces involved. Dean (1895) repeats one of these illustrations and makes the following statement concerning such movement. "It is the pressure of the fish's body against the water enclosed in these incurved places which causes the forward movement." The forward motion is certainly attained, as Dean wrote, by the pressure of the fish's body against the water and in the following manner. The mechanical forces brought to bear on the water are diagonally backward as indicated by the small arrows in the diagram (Fig. 39 A). As these are distributed symmetrically[3] about the line of progression, a forward resultant of re-

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[3] This does not mean that the planes of pressure are at all times paired, from side to side. There may be an excess of not more than one on either side, but as soon as that one passes off the tip of the tail, the excess appears on the other side, so that, considering time as an element, these sine curves may be considered symmetrical about the axis of motion.

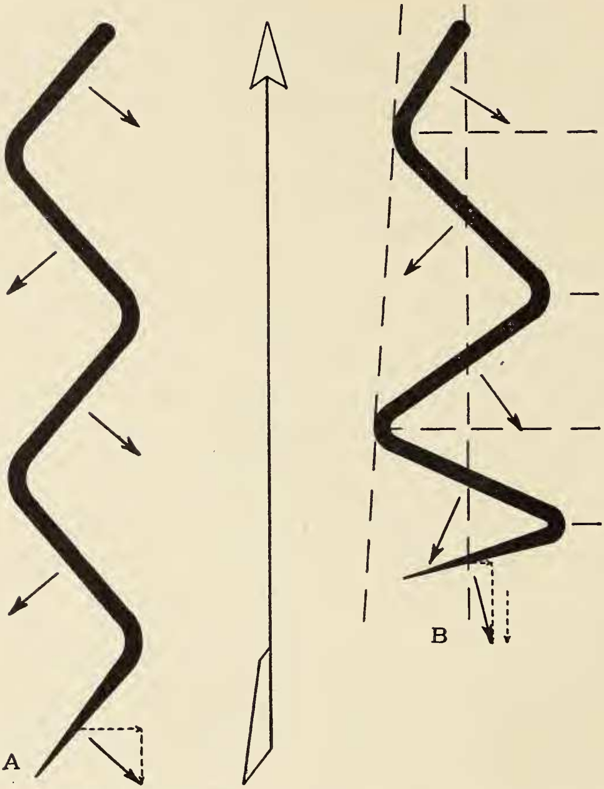

Fig. 39. Diagram of anguilliform locomotion. The feathered arrow indicates the direction of progression. The short dark arrows indicate the direction of pressure from the backwardly moving waves. The dotted arrows indicate the vector quantities. A, the simple basic action of anguilliform locomotion. Note the relative sizes of the vectors. B, the increase in amplitude and decrease in wave length as generally employed. Note the relative sizes of the vectors as compared with the effective vector of A. The transverse dashed lines indicate the posterior decrease in distance between the crests, and the longitudinal ones the accompanying increase in amplitude.

action follows as is indicated by the feathered arrow, for pressure from a moving plane is always at right angles to its surface.

It might be objected that as the eel is moving ahead there is likewise adverse pressure diagonally forward from the anterior sides of these backwardly moving waves. The truth of this is evident and it simply makes it necessary for the fish to pass these waves posteriorly at a rate considerably faster than it expects to move forward. Cinematography has proven in certain cases, at least, that in comparatively slow movement the waves travel at over twice the speed attained by an eel in its forward progression.

The speed of the waves moving backward must exceed that of the forward motion of the animal as a whole. If the two speeds just equalled each other, it would mean that any point on a wave, such as its crest, would be stationary with reference to the sea bottom; but as one is dependent on the other this is obviously impossible. The difference in the two speeds is greater than that theoretically necessary on account of other factors, due to what in machines would be called mechanical imperfection.

Maurey (1895) dismisses a certain interesting point with this statement, " . . . the undulations of the tail are . . . . more pronounced than those of the rest of the body." By "tail" it is taken that he means that portion of the fish posterior to the vent. This is perfectly true but prompts further analysis. The change that actually takes place in the waves in progressing backward is that their amplitude increases and the distance between the consecutive crests decreases, as diagrammed (Fig. 39 B). Both these changes operate to effect movement more efficiently, for as indicated (Fig. 39 A and B), the vector quantities of force shown by the small dotted arrows vary as these two aforesaid factors become greater and less respectively, the effective vector force becoming relatively greater. There is a further advantage in this on account of the anatomical structure of eels in that they are nearly cylindrical anteriorly and well flattened posteriorly; for, because of internal stresses and strains, a ribbon shaped piece bends more readily (transversely) than does a cylindrical one. Furthermore the viscera are all contained in the anterior rounded portion whereas the caudal portion is devoted mainly to musculature. Also more thrust may be had from a blade-like structure than from a cylindrical one (the diameter of which equals the width), in that it presents its surface more effectively to the water, so if for no other reason the emphasis is placed on the posterior portion. As the myomeres carry on the waves, each one, as noted on page 167, gives its little added impulse. These added impulses appear to be in excess of that needed to maintain the original curve to the end of the tail and so they keep increasing the amplitude and decreasing the spaces between the crests of the waves until the tail's tip is reached. The diagram of this (Fig. 39 B) is purposely exaggerated for the sake of clarity, for actually the changes noted are often slight, an instantaneous photograph sometimes being necessary to establish their presence.

Ostraciiform Movement: The type of locomotion here dis-

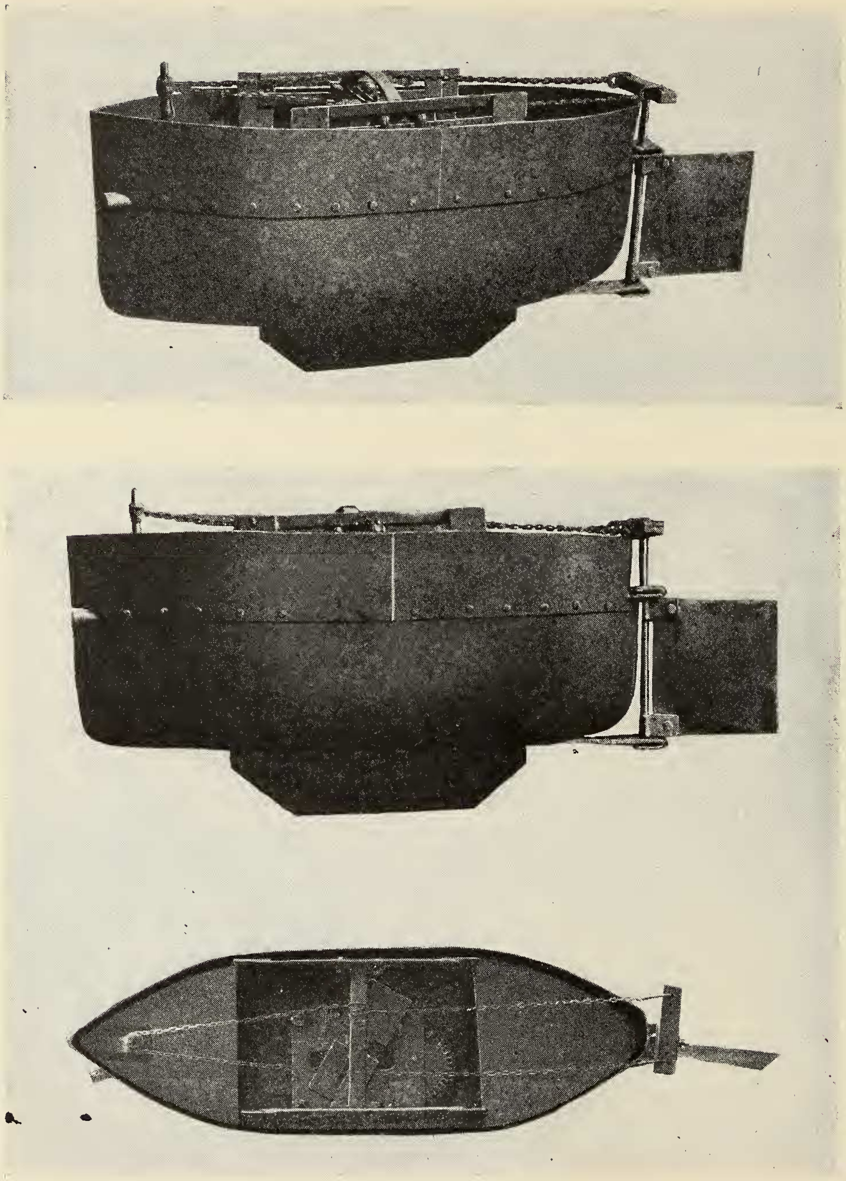

Fig. 40. The ostraciiform model. Perspective, side, and plan views.

cussed is illustrated well by the Ostraciidae and represents the opposite extreme from that of the anguilliform. It has been the center of considerable controversy, for it has been argued to be physically impossible to obtain a continuous forward thrust from this sort of movement. Since the Ostraciidae are incased in hard and unflexible tests it is obviously impossible for them to pass waves posteriorly as do the more flexible fishes. The tail protrudes from an opening in the test and is supported on a peduncle too short to be thrown into waves and is therefore insufficient to give any efficacious movement of the anguilliform type. In these fishes the locomotor emphasis is placed on the pectoral fins and other parts while the tail is used primarily as a rudder. However, at times when more than ordinary speed is required, the tail is given the only motion possible, a lashing from side to side. Borelli (1680) argued that such movement in itself was sufficient for locomotion and stated it as the basis of general fish progression. Pettigrew (1874) claimed this view to be erroneous, and stated that some flexure or turning over of the body was necessary. His logic would seem to be correct but that he was in error has been positively demonstrated by the construction of a model (Fig. 40). Here only a side to side swing was possible for the "tail fin," but nevertheless this mechanical contrivance moved forward with a sure and steady gait. The failure to include a certain elusive factor apparently led him into this error.

Although the fact that such a device will move forward is generally recognized by physicists, a discussion of the behavior of the model will serve to illustrate better why motion of this kind will produce a forward component. Fig. 41 shows diagrammatically how this model starts off and picks up speed until its maximum is reached. The first swing of the tail does not appear to produce a backward component as might be thought and as Pettigrew reasoned, but being a simple bending at the pivotal point, swings the nose as is indicated from position 1 to position 2. That this is true may be shown by grasping a sculling oar, located centrally, and giving it a swing to one side. The boat will show no tendency to back up but will swing around to a position similar to "2" in the figure. It may be here pointed out that this is the elemental basis of sculling and only because of this fact is it possible to move a boat forward in such a manner. In fact a skiff may be sculled

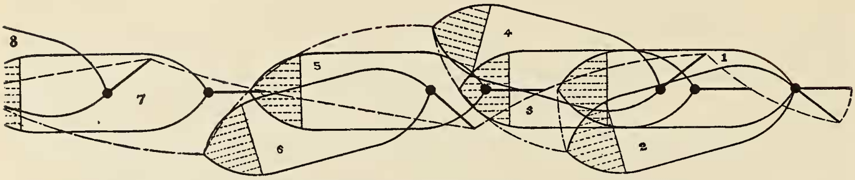

Fig. 41. Diagram of the movements of the ostraciiform model. Eight successive positions are shown. The dashed line indicates the path of the tail's tip and the dot and dashed line that of the nose. Position 1 is that of the model at rest and 5 the return to the initial position after passing through one complete cycle, 2, 3 and 4 being intermediates while 6, 7 and 8 are repetitions of them but separated more widely on account of the increasing speed as the model gets under way.

by simply pressing the blade from side to side in a manner identical to that of the model's "tail," the other motions of a skilled sculler making for efficiency and ease on account of the structure of the boat and its position *on top* of the water. Pettigrew tried to explain this away in a roundabout and confusing fashion. The twisting of the wrist which tips the blade from side to side with each stroke serves the simple function of holding the oar in the oar-lock. Fig. 42 shows this diagrammatically. If the relation of the stroke and the angle of the blade is reversed, as in the dotted position, the oar jumps out of the oar-lock, as all beginners at sculling can testify, for the pressure of the water is diagonally upward instead of downward at the oar's tip. Other "fancy" movements of skilled scullers may make for efficiency in various ways but the fundamental principle remains the same. The following continued description of the action of the model serves to elucidate further the action of the sculling oar as well as the tail of rigid bodied fishes. The model now in position 2 (Fig. 41) is sent forward by a return stroke, as the tail presses diagonally backward. By the time the nose has reached the axis of progression the tip of the tail has also, and the model is as in the initial position, but advanced to 3, and is now moving forward by inertia so that by the time 4 is reached it is further along but is gradually slowing down. From 4 it shifts to 5 and from 5 to 6 and 7 and so on, with the nose wig-wagging and the tail beating. The factor which Pettigrew misunderstood or failed to recognize is this oscillation of the anterior part. It is hardly necessary to point out in this connection that a freely supported body such as a boat or a fish if jointed as described has no rigidly fixed pivot (in space) to work on but either part may be considered as bending about the other.

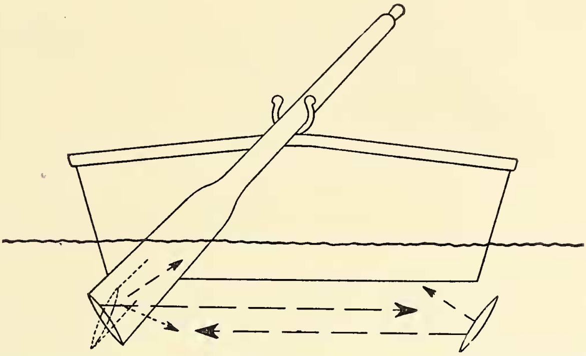

Fig. 42. Diagram of a sculling oar, viewed from the rear. The horizontal dashed arrows indicate the path of travel of the blade. The angle the blade makes with the surface of the water is indicated on both sides of a stroke. The pressure is indicated by the arrows pointing diagonally upwards. The dotted blade indicates the position which causes it to rise out of the oar-lock and the dotted arrow indicates this pressure.

The movement thus obtained is very close to that of the trunk fishes as in such forms a sharp contraction of the lateral muscles inserted in the peduncle first on one side and then on the other suffices to produce this action. The greatest difference between such a fish and the mechanical model described is that in the latter there is a single joint about which the fore and aft portions turn whereas in the former a series of a few joints (in the vertebral column) cause a broad curve to be formed as each vertebra bends on the next adjacent one. This, of course, is merely a quantitative difference as pointed out on page 171.

In addition to the explanation given above, a rearward flow (or a forward motion) is automatically induced by the back and forth oscillation of even a rigid tail piece. A mechanical analogy may be made by placing a cue flat on a billiard table, with a ball in contact near the handle end. If a swinging movement be imparted to the cue with the butt end as a pivot the ball in addition to its lateral path will travel relatively rapidly along the length of the cue away from the center of rotation. This is true irrespective of the speed at which the cue is moved.

An important point not considered as yet bears on the impingement of a flowing stream of water on a moving blade, in that on striking a surface it spreads out and follows it as a sheet flow. However, the alternate striking and drawing of a particle of water causes it to travel backward in a zigzag line progressively more and

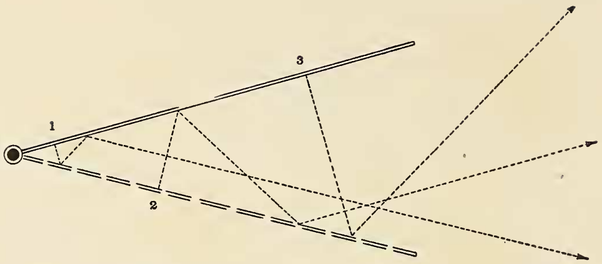

Fig. 43. Diagram of the path of particles of water about a rigid tail fin. The dotted lines indicate the paths of three particles of water starting at various points along the fin. The original thrust is indicated as though at right angles to the plane of pressure. The initial path would not be quite at right angles to the plane because of the circular motion of the blade but is so shown here for the sake of charity. Note that the particles starting near the pivotal point attain a more nearly straight backward thrust than do those starting further back.

more nearly parallel to the axis of progression. Fig. 43 diagrams this. Under this action the particles follow the paths in the diagram under the constant urging of the blade only. For example, if any point be taken on one of the paths and connected with the pivot, it will give the position of the tail when the water particle is at that point. The breeze from the edge of a fan will demonstrate the truth of this, for otherwise a fan would fail in its purpose. This action coupled with the fact that the fin is curved, gives a nearly backward thrust, greatly increasing the effective power and reducing the swinging of the head to a minimum.

The relative size of the body and tail of course, influence the speed, as do the amplitude of oscillation of the tail, the shape of the body and many other similar factors. The exact mechanical relations of these various elements are outside the province of the present discussion, but doubtlessly they could be reduced to and expressed as formulae, varying with each form.

A piece of apparatus made so that the two parts (body and tail) were exactly equal in size, shape and weight would fail to move forward at all, simply remaining in one place while bending and re-bending upon itself. This may be observed sometimes in terrestrial insect larvae. Occasionally a caterpillar, very similar fore and aft, in its efforts to extricate itself from a puddle, will violently bend from side to side so that the arch occurs centrally with no progressional movement at all.

The greater inertia and resistance to motion sidewise through water of the larger part of the model, referred to above as the body, causes it to move through less of an arc than the lighter and more mobile tail portion, which fact tends to keep the model or fish on a true course and causes the force to be expended in a backwardly direction, as forward is the path of least resistance.

Carangiform Movement: The movements displayed by most typical fishes are intermediate between the two extremes just examined and the more generalized members of the family Carangidae, such as *Caranx*, occupy about the middle position in this respect. Many fishes do obviously never throw their bodies into a series of reverse curves as described under Anguilliform Movement nor are their bodies hard and completely inflexible as in the case of the Ostraciidae, but the entire body flexes as from a pivot (or fulcrum) at the atlas. As in *Anguilla*, the first act preparatory to locomotor effort is the contraction of the first few anterior myomeres on one side. The head being less in bulk and offering slighter resistance to the water than the rest of the body, moves through

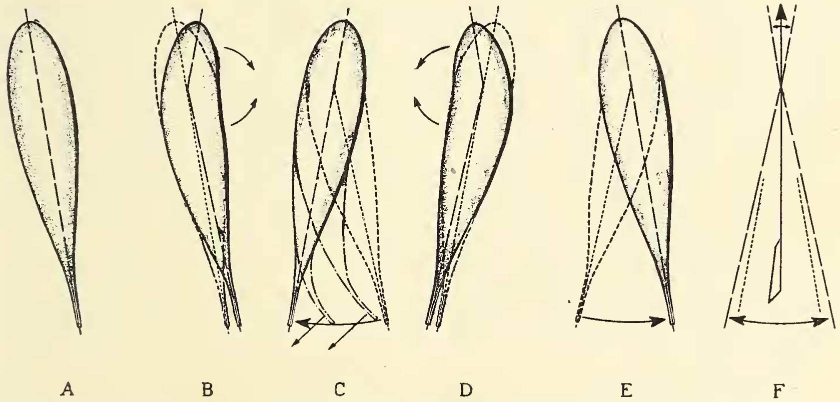

Fig. 44. Diagram of carangiform locomotion. The positions are serial from left to right, with the preceding indicated by dotted lines for comparison. A, the initial or resting position. B, the contraction of a few anterior myomeres on one side. Note the great deflection of the head and the slight deflection of the body and tail. C, the continuing backwards of the metameral contractions with relaxations immediately following swings the tail as shown. Here two intermediate positions are indicated. The fish is now in a similar but opposite position to that of A. D, Identical but opposite to B. E, Identical but opposite to C, completing one cycle and returning the fish to A. F, a composite of the movements of the preceding five positions indicating the amplitude of the caudal and cephalic oscillations. The lower dotted lines indicate the head's oscillation, projected. The feathered arrow indicates the axis of progression.

Fig. 45. *Caranx* superimposed on *Anguilla*, indicating the similarity in movement and the abbreviation of the one over the other.

the greater arc and may be said, relatively, to be thrown to one side, as a result of this primary contraction. The myomeres then successively contract and relax caudad, bringing the tail to the axis of the head with a powerful sweep. Fig. 44, A, B and C, diagram this in a series of positions viewed dorsally. Because of the pivotal point being at the base of the skull a short swing of the head is all that is necessary to place the tail in a position for a long telling stroke. Fig. 44, D and E, complete the cycle to the other side and thus the fish returns to the original position. F is a composite of the movements showing the amplitude of the caudal and cephalic oscillations. While both the caudal and cephalic axes cross the axis of progression, the former is always moving toward the axis of the head, while the latter is always moving away from the axis of the body. This is possible because of the constant shifting of these two axes, which, as we have seen, reaches its maximum prominence in the Ostraciidae. Fig. 44 C shows two intermediate positions of the body and tail in making a stroke, and clearly indicates its relationship to the anguilliform type of movement, while the other parts of Fig. 44 show equally well the relationship of the carangiform to the ostraciiform. Fig. 45 in which *Caranx* is superimposed upon *Anguilla,* serves to illustrate that the movement of the body of the former is simply an abbreviated form of the latter, in which never more than one half of a sine curve is formed.

It should be noted here that while the pivot is at first at the atlas, it moves backward (as the point of greatest curvature) with the sweep of the body and tail so that near the end of the stroke it is nearer to the tail than to the head. This is especially advantageous for at first the anterior part is relatively short while later the posterior part is. From this it should be evident that an advantage is had over the ostraciiform type in which the pivot is fixed well behind the middle of the body. Likewise an advantage is had over the anguilliform type, which possesses what may be considered multiple pivots, a condition in which this advantage is practically lost.

Comparison and Discussion: The preceding outline of the action in the body movements of the two extremes (Anguilliform and Ostraciiform) and the norm between them (Carangiform) makes it now possible to discuss in some detail the various characteristics of the results of progressive metameral contractions as seen in fishes generally. There is such a complete gradation through these three rather arbitrarily chosen types just described that it is impossible to say where one leaves off and the other begins. In fact, the anguilliform type might be considered, in a sense, as a great number of ostraciiform units arranged serially, or the latter as an abbreviated form of the former. A fan in oscillating is analogous to the ostraciiform movement if rigid, but if sufficiently elongate and flexible the same driving power produces an anguilliform (flag waving) movement. It is obvious that these differ only as do their proportions and the flexibility of the oscillating members.

This series includes all fishes that have a functional tail, that is, one which is capable of being swung from side to side in locomotor effort whether it is habitually so used or not, and it excludes only such unorthodox forms as *Hippocampus*. Further, it might be shown by means of a statistical curve of variation that the carangiform type of movement is the one most frequently encountered. That is to say, fishes of that type would roughly form the mode while the anguilliform and ostraciiform would fall at either end of such a curve. All others would come between these in increasing frequency as the mode is approached. Furthermore, the carangiform method is pre-eminently fitted for speed and appears to be of the highest efficiency, since it always accompanies fishes of high speed, such as *Pomatomus*, *Scomber*, and fast oceanic forms generally. The other two types are both principally methods of comparatively sluggish littoral forms. The ostraciiform motion is usually used only as an auxiliary to other locomotor efforts not concerning the trunk proper, while the anguilliform is typical of fishes such as the thigmotactic eel and moray, although these are capable of speed utterly unknown to the passive trunk fishes and are even occasionally to be found among the pelagic fauna as in the case of the Ophidiidae.

Doubtless locomotor characteristics in general have a con-

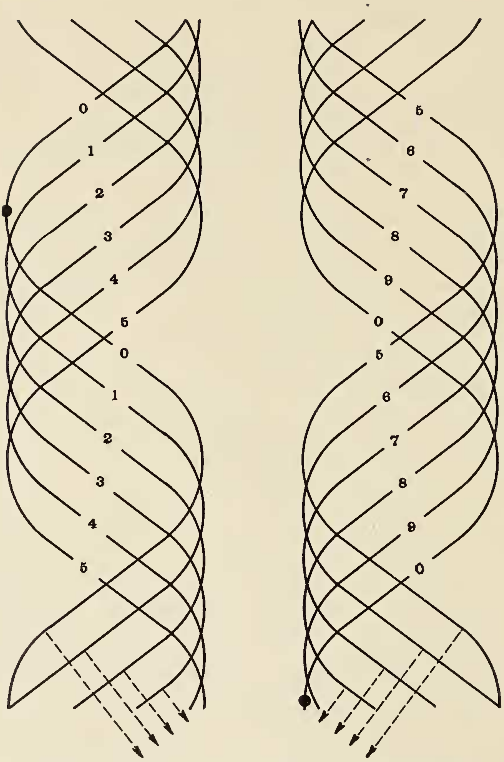

Fig. 46. Diagram of the continual backward push of the caudal. Each curved line represents the vertebral axis of an anguilliform fish. Ten successive positions are shown numbered from O through 1 to 9 and back to O. The diagram has been broken in two simply to avoid a confusion of lines, 5 in the left, being identical with 5 in the right. Note the dotted arrows indicating that the push of the tail's tip is always diagonally backward. There is no "non-effective" stroke. The dark disc on line O in the left half is the same as that on O in the right in reference to the wave motion and indicates the distance that one wave has traveled in passing through the ten successive positions. The direction of motion is opposite to the travel of the waves.

siderable phylogenetic significance. However, the great frequency and extent of parallelism and convergence among widely different groups due to the direct contact of such plastic animals as fishes with such a powerful environmental factor as similar locomotor needs, shows that no great importance should be attached to the grosser movements of the trunk and tail as indicative of close phylogenetic relationship.

That the tip of the tail, no matter which direction it is moving in, is continually "pushing" water diagonally behind is made clear in

Fig. 46 wherein is represented a series of positions of the tip of the tail showing how it is always presenting a backwardly moving plane. An anguilliform type is represented, but it is obvious that it is equally true for the others. In the case of the ostraciiform type the difference is more of quantity than of kind, as no matter how short the projecting peduncle is, there still remains a few myomeres to operate in the conventional manner as far as interfering circumstances permit, and the tail fin is always flexible. As pointed out in the diagram of the ostraciiform model in motion, in this device the second half of any stroke is entirely concerned with swinging the nose and does not have a forward thrust on account of the mechanically rigid tail piece. This clearly never obtains completely in nature on account of the flexibility of caudals but doubtless is Pettigrew's "less effective stroke."

The preceding paragraphs show that these three designated types of body movement are in reality nothing but varying forms of the same rather involved motion, differing only on account of the differences of shape of the body in which the metameral contractions occur. They are broken up here only for purposes of analysis.

Pettigrew (1874) states that fish always throw their bodies into two opposite and complementary curves, which is necessary to his explanation. This is at least conceivable for many forms, but is never done by *Caranx* and a host of others. Simple observation will suffice to prove this. He further intimates that as the tip of the tail moves away from the axis of motion it is impeding progress, and drags in such absurdities as having the fish roll over slightly so as to present an oblique blade to the water. Large sturgeon when swimming slowly, especially when starting off, have a noticeable roll, which is partly due to the fact that the small vertical fins have only slight powers of steadying; the stabilizing effects of which are explained under "Reomorphism." The reason for this roll is purely a mechanical one and the action is seen in the ostraciiform model when starting, especially before the nose has attained its full swing. It is apparently this movement that he construed to be a voluntary turning over, although how it is supposed to be voluntarily accomplished is not indicated.

Pettigrew further writes that the mackerel twists its tail to such a degree as to be "very much after the manner of a screw in a steamship" and thus "to drill the water." Observation confirms this in no way whatsoever, and a great many more objections could be raised to other parts of his explanation, which, however, may be passed over here. Probably the most remarkable part of it all is the lack of criticism that he has had. Du Bois-Reymond (1914) touches on Pettigrew's work, showing some knowledge of the ostraciiform effect, but leaves the subject essentially as it was. Bridge, in the Cambridge Natural History (1904), in dealing with locomotion, simply paraphrases Pettigrew, thus giving the latter's views a very wide circulation.

The movements have thus far been considered only in reference to the fish itself and have not been referred to the water through which the fish is moving, except in the case of the ostraciiform model. Fig. 47 diagrammatically represents the motion of a carangiform fish relative to the surrounding medium. It is to be noted that the path is truly rectilinear. The boundaries of the single hatching represent the limit of oscillation of the tail's tip induced by the metameral undulations. Those of the double hatching represent the limit of the snout's swing. The track or path through which the fish moves is rectangular in cross section, if viewed end on. That the head makes a much smaller sweep is indicated by the double and single hatching. The initial position in which the fish is shown is the same as C (Fig. 44), and the head is ready to be flexed to the left. Assuming the fish to be already in motion, the nose is brought to cross line 2 and the tail to 2′. The body is then in position for a really effective stroke which runs the fish forward to position 3 and 3′, after which the other half of the cycle is completed, bringing the fish to 5 and 5′. In this diagram momentum has been omitted for the sake of clarity as it is quite obvious that the thrust from the body and tail would carry the fish along at scarcely diminished speed while it wagged its head in order to give a stroke from the other side. Also it is clear that the stroke of the body and tail must tend to deflect the head toward the midline, the direction to and beyond which it is to go at the finish of the stroke. It is to be noted that most of the time the head is either travelling on the right or left limiting boundary, the path being indicated by the dot and dashed line, while the tail is occupied for the most part in passing from side to side, except for momentary touchings of its limiting lines on either side, indicated by the dashed line,

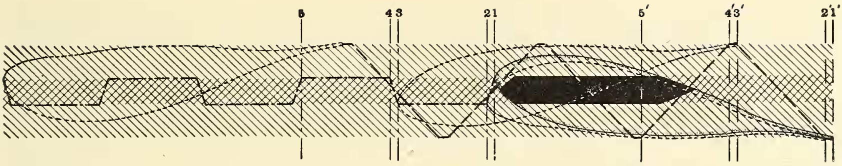

Fig. 47. Diagram of the movements of a carangiform fish. Four positions are shown. The dashed line indicates the path of the tail's tip, and the dot and dashed line that of the nose. Position 1–1′ is identical with C of Fig. 44, 2–2′ with D and 3–3′ with E. This represents one-half a cycle, the remaining positions not being shown except the one at the extreme left which is 4–4′ (B of Fig. 44) of the next cycle. Momentum and increasing speed have been omitted for the sake of clarity. The single hatching indicates the extent of the amplitude of the tail's swing and the double hatching that of the nose. The black area indicates the orthokinetic part.

while the head is switched to the same side with which the tail is in contact. This is in agreement with observation, as it means that the head is comparatively quiet in its oscillation while the caudal portion appears in violent motion and actually is, for, in addition to the above relative movement, it swings through a wider arc. A mackerel swimming rapidly shows the posterior portion of the body simply as a blur, while the head can be seen simply weaving from side to side ever so slightly.

While most of the fish's body is oscillating over a shaded area in one way or another, there is a point about at the atlas which travels directly forward in a straight line. That portion of the body that does not leave the boundaries of the double hatching at any time, indicated in black, represents a solid core of the fish's body which is continuously concentric about the axis of motion. The remaining parts are occupied first on one side and then on the other part of the track, which is shaded. It is plain that it is not always the same exact materials which occupy the central core, but this variable core, always the same in bulk as long as the fish swims by means of similar oscillatory movement, is the only part of the fish which actually goes continually forward without making a waved track through the water leaving alternate unoccupied areas on either side. This section may be called the *orthokinetic part.* The parts which oscillate about this section, anteriorly and posteriorly may be called respectively the *cephalic amphikinetic,* and the *caudal amphikinetic parts.*

It is unnecessary to figure the anguilliform movement in this manner for it follows that if a long produced form occupied the place of the fish in the diagram, similar paths of motion could be traced about it. The orthokinetic part would bear the same relation to the fish and there would be no second or third as might be supposed, because of the numerous crossings of the axis of motion made by the sinuous body. As the undulations are passed backward, a series of sections of the fish alternating with interspaces would follow this path but would produce a no more continuous section than would the sidewise movement of the head and tail. However, if the undulations were so slight that the crest of any wave never caused the body to pass completely to one side of the axial line, the orthokinetic part would be considerably attenuated. This probably seldom happens in active swimming. On the other hand an eel violently agitated may thrust the head from side to side in such amplitude that no orthokinetic part at all is formed. When this takes place, which seems only to be at times of mortal danger, except in greatly compressed forms, the progress made is not proportional to the apparent energy expended and the fish usually soon resorts to the more normal method of slipping along. Therefore it is believed that this is an abnormal effect caused by the over stimulation of great danger. It is doubtful if such locomotion is nearly as effective as when the orthokinetic part is allowed to remain intact. In the ostraciiform model the point that moves forward continually is, of course, at the joint (Fig. 41), for this point in each position is on the axis of progression. It would therefore seem that the anterior placement of the orthokinetic part is associated with the efficiency of locomotion through water by means of body undulations.

The foregoing analysis of the differences and similarities of the three phases of the body movements of fishes induced by metameral contractions may now be contrasted in the following table:

TABLE I

Anguilliform	*Carangiform*	*Ostraciiform*
1. Cephalic amphikinetic part moves imperceptibly or very slightly from side to side, normally.	1. Cephalic amphikinetic part moves through a considerable arc, and its alternation with the body and tail movement is generally observable.	1. Cephalic amphikinetic part moves through a large arc, but there is no alternation, the nose shifting with the tail.
2. More than one-half a sine wave is formed by the body, typically several entire waves.	2. Not more than one-half a sine wave is formed by the body and frequently it is anatomically impossible to form even that much.	2. Hardly any curve is formed at all by the small peduncle, simply a swing from side to side being obtained.

3. The pivot is at the base of the skull.	3. The pivot is at the base of the skull at the beginning of a stroke, but migrates backward with it.	3. The pivot is at the base of the caudal peduncle.
4. The orthokinetic part is concentric about the axis vertebra but is followed by a number of backwardly moving sections. It may even be absent.	4. The orthokinetic part is concentric about the axis vertebra, but is not followed by any sections.	4. The orthokinetic part is concentric about the vertebrae at the base of the peduncle.

This table may be taken as indicative of the characters by which the three forms of body movement are defined and by which the dynamic metameral characteristics of a given species may be recognized, for it is to be thoroughly understood that they simply represent phases of the same thing that have been forced on fishes in response to their changes in bodily form, often by evolutionary factors not directly concerned with locomotion.

Special acts of the tail fin relative to rectilinear movement but not the result of the cumulative metameral contractions are discussed under the head of "Movements of the appendages," and their form under "Reomorphism," but the importance of the tail to generalized fishes may be considered here in relation to its motion induced by the cumulative effects of the metameral body muscles. This cumulative effect of the lateral musculature gives the tail a wide swing and in so far is effective in much the same way that it is in the ostraciiform type; moreover the tail, being flexible, carries out the movement of the rearward-traveling waves by momentum; but this movement is modified by the differential forces at work on the tail incident to its motion. The functional significance of the tail is indicated by the following experiments made on *Scardineus erythrophthalmus:*

Experiment 1. The tail fin from one example was carefully amputated. The fish was then placed in a trough eight feet long together with an entire example of equal size. As usual, these two fish rested side by side at the far end of the trough. Carefully approaching this end, a smart blow with the flat of the hand was delivered against it, which sent them scurrying to the other end where they took up similar positions. Each time that this was tried, they arrived at the distant end apparently simultaneously after traversing the intervening distance side by side. The only obvious difference was that the example minus the tail oscillated the body faster and through a greater arc. This might be taken as a measure of the efficiency of the tail, making a greater effort incumbent on the mutilated fish in order to keep abreast of the normal one. However, it is doubtful if the normal example was travelling at much less than top speed since none of this species has been seen to travel measurably faster in an eight foot run under any circumstances. For simple mechanical reasons the change in oscillations would be expected to take place. The greater resistance of the tail to movement from side to side being removed, with similar exertion it would follow that a wider arc or more abrupt curve would be passed through by the stump, and at a higher rate of speed. This increased speed of the lessened area of pressure moving by means of the same muscle mass appears to offset to some extent the difference between it and that of a slower motion with a greater functional pressure area. However, in a longer run there is no doubt, that a marked difference would appear in the time required to cover a given distance.

Experiment II. The tail of another fish was immersed in liquid air, which instantly killed and made rigid the portion so treated. The film of ice formed about the tail tended to make the fish float up, but aside from this inconvenience it was obvious that the wig-wag of this now rigid fin was extremely inefficient. A series of individuals were so frozen as to make each successive one rigid a little more anteriorly. A regular decrease in speed was noticeable, until all myomeres were frozen and motion ceased. To demonstrate that it was the mechanical effect of a rigid tail, and not nervous inhibition incident to freezing that caused the above result, the fore part of the head of one fish was frozen, with ice solid in the gill and mouth cavities. Strangely enough this fish showed no prominent reduction in speed. Further, in thawing out, fishes partially frozen from the posterior end, resumed some of their former speed although the frozen section was lifeless and flexed only because of the movement transmitted to them by the live anterior myomeres.

Experiment III. In other examples the nerve cord was severed just past the viscera in such a manner as to paralyze the posterior portion. This caused a slight slowing down which is believed to be proportional to the number of myomeres cut off. The deadened portion oscillated as before, however, on account of the continuing effect of the ripple started anteriorly, although of course the efficiency was less. These results were practically identical with those obtained by thawing tails after freezing them in liquid air, as in Experiment II.

Experiment IV. In still another example, the body was made rigid by passing a fine steel wire parallel to and above the vertebral column to a point just behind the brain case. This succeeded in inhibiting the undulations and locomotion almost ceased. A very slight forward movement was produced by wagging the head and tail fin, which the wire did not prevent. On removal of the wire, locomotion proceeded as before.

The inference drawn from these experiments is that the metameral contractions and the resulting flexures of the body act independently and directly on the surrounding medium as well as by their cumulative effect on the tail fin, the importance of which is entirely based on its terminal position. The significance of this seems never to have been stated, although it is clear from the above four experiments that by far the greater effect is due to the contracting myomeres themselves, rather than to the tail fin; this is especially evident by experiments I and IV. See Breder (1925b) for other similar data. The relative importance of the tail fin varies with its shape and size as well as the amplitude and wave length of the body oscillation.

Regnard (1893) found that the pull on a tow line of a *Cyprinus carpio* was reduced by one-half by removal of the tail fin. This is questioned, for similar experiments failed to yield the same results, this being found a very unsatisfactory method because of induced nervous inhibitions. Also, the subjects suffered from exhaustion very rapidly, usually giving a few vigorous tugs and then sulking. It would seem that after such an operation, a measured pull could be easily half as great on account of many causes aside from the simple loss of the tail fin.

Movements Of The Appendages.

Movements of the appendages are more generally concerned with maneuvering than with locomotion in a straight line. However, there are numerous forms representing different locomotor types in which all fins (except the pelvics) have been so modified as to be the primary locomotor organs. Further, most species commonly using the more primitive locomotor method, body undulation, also use the fins at times for inducing forward movement, especially for slow, short travels. In some, two or even more methods appear side by side so as to provide multiple locomotor systems to be used either together or separately. In fishes which seldom, if ever, use body undulations, the same general body form is retained, unless they are of exceptionally slow movement, for it is primarily the necessity of conforming to streamline effect that shapes them.

Various fins of numerous fishes are capable of being undulated for purposes of progression. These movements are comparable to the undulations of the body examined under the heading "Body Movements." Certain of these are nearly the same in application (those involving the longitudinal fins), while others (those involving the caudal and pectoral fins) introduce other elements. That is,

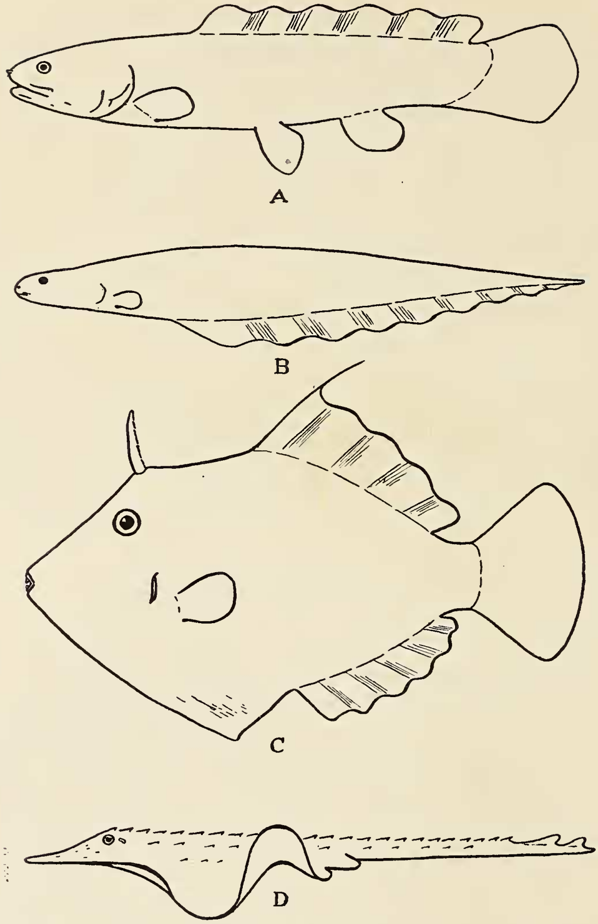

Fig. 48. Undulation of the longitudinal structures. A, *Amiatus*, dorsal undulation. (Amiiform). B, *Gymnotus*, anal undulation. (Gymnotiform). C, *Monacanthus*, inclined dorsal and anal undulation (Balistiform). D, *Raja*, pectoral undulation, (Rajiform).

in many forms the undulations of certain fins may be considered as localized parallels to the body movements of other forms.

Longitudinal Structures: The dorsal and anal fins in certain fishes carry on wave movements which affect motion in a manner similar to that caused by anguilliform movement, although of a gentler sort. Usually in such forms undulations of the body are resorted to when a higher speed is desired. *Amiatus* is an excellent example of the type which shows undulations being carried on in the dorsal fin. This may be called *Amiiform* (Fig. 48 A). However, as above noted, this species undulates the entire body for rapid movement in a manner intermediate between anguilliform and carangiform locomotion. *Gymnotus*, on the other hand, has the seat of similar undulations in the anal fin. This may be called the movement *gymnotiform* (Fig. 48 B). *Balistes* shows this form of movement in both dorsal and anal fins, each being inclined a little from the horizontal, but oppositely, so that their resultant causes a forward movement. This may be called the *balistiform* movement, (Fig. 48, C). In these longitudinal fins the waves are propagated by simply moving the rays from side to side serially in a method analogous to the anguilliform movement. This has been demonstrated by a model (Fig. 49), which incidentally may serve as a mechanical representation of the anguilliform motion as well. Instead of myomeres contracting to bend the body, muscles attached to the sides of the fin rays at their bases contract, so deflecting them alternately from a vertical position in the appropriate manner. *Raja* represents a slightly different sort of longitudinal undulation. Here the greatly expanded pectorals effect a similar end but operate in a vertical plane. Maurey (1895) illustrated these movements beautifully by serial photographs. This may be called *rajiform* movement (Fig. 48, D). It is to be noted that longitudinal structures used in this manner are practically without anterior stiffening. That is, fishes with spines in the dorsal or anal fins do not undulate those fins. In such examples where spines are present they are entirely free from the rayed and undulating part of the dorsal, as in *Balistes*. However, in this case there is a slight thickening of the anterior rays which is discussed below.

In addition to fishes using longitudinal structures in an anguilliform manner, others, chiefly with short fins, use them in what we may consider an ostraciiform manner. *Lagocephalus* and *Spheroides* often so use the dorsal and anal as a unit, simply flapping them from side to side. This may be called the *tetraodontiform* movement. (Fig. 55 A). These fins may be thought of as an ostraciiform tail in two parts moved slightly forward dorsally and ventrally. The slight divergence from straight ahead of the reaction, owing to the positions of these fins, is, of course, compensating. In those used in this manner there is a tendency to a thickening or stiffening of the anterior part of the fins.

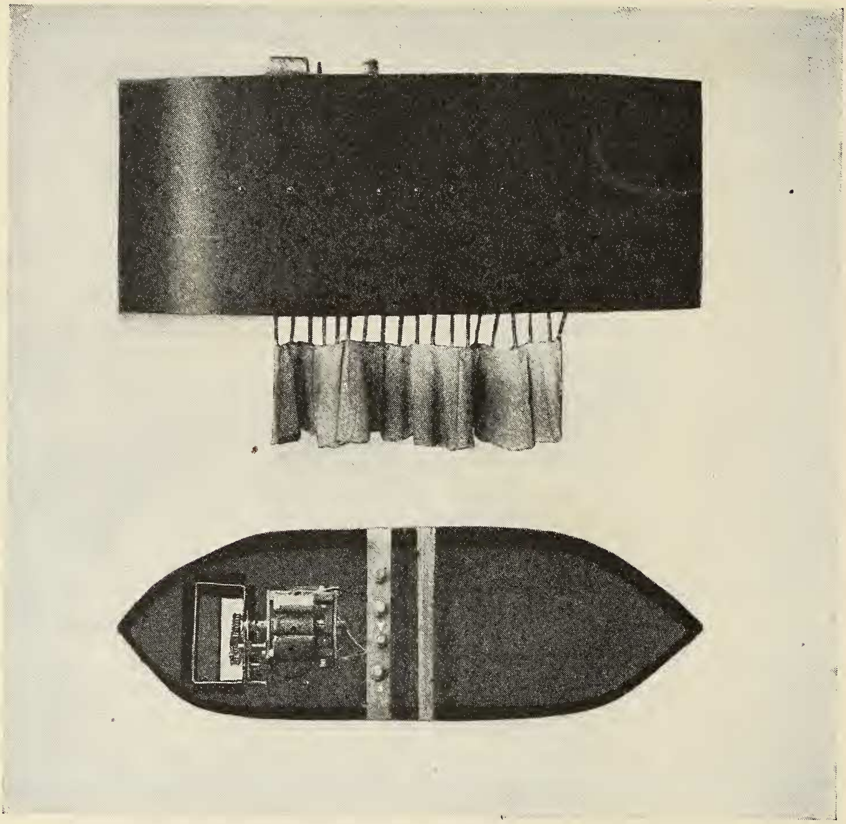

Fig. 49. The anguilliform model. Side and plan views.

Between the anguilliform and the ostraciiform extremes there are intermediates, although it would serve no useful purpose at this point to consider any as carangiform. The thickening of the anterior ray of the dorsal and anal of *Balistes* shows a tendency toward an ostraciiform fin movement, and indeed not infrequently does it flap these fins as units instead of undulating them. This thickening of the anterior part of such fins seems also to be associated with angular divergence from the axis of motion, whereas in such forms as *Amiatus* and *Gymnotus,* as previously noted, in which the longitudinal propellor is practically parallel to the axis of motion there is no such thickening.

Caudal Undulation: While the caudal is operated primarily by the action of the body muscles, many fishes at times may be seen to undulate the tail fin vertically and move forward slowly without any other apparent effort. These waves travel at right angles to the undulations of the longitudinal structures and might be expected to raise or lower the posterior part of the fish. Observation shows that such is not the case, other factors entering which translate the thrust into a forward one. One difference is that the rays are convergent instead of parallel. Considering each ray separately, in waving from side to side, it naturally has a forward reaction of the ostraciiform type. The fact that about one half the number operates in an opposed manner to the other half causes a double effect which obviates the necessity of a head oscillation. This may be roughly likened to the squeezing of an orange pip between the fore finger and thumb, the considerable force attained by pressure on its inclined sides being not altogether different from the pressure of the alternate rays. Of course, in the latter the rays are not directly opposite and a solid and a fluid are considered instead of two solids, the efficiency being much less, but this may help to visualize the effect.

What little thrust of a similar nature acts to press *Amiatus* downward and *Gymnotus* upward on account of their dorsal and anal fins (with parallel rays) respectively, is inconsequential because of the difficulty of moving a streamline form at right angles to its intended direction, just as the little vertical thrust derived from the present method dissipates itself. A slight twist of a fin, practically imperceptible to the eye, would readily offset any such action. Du Bois-Reymond (1914) states that fishes often obtain a thrust from the tail by moving the inferior border to one side and the superior to the other. This is not quite the same as the above described undulation. The central ray of the tail remains still and simply twists on its axis in the latter, while in the former all rays pass through a complete cycle of oscillation. In the method described by Du Bois-Reymond, the upper part of the tail is given a backward thrust diagonally to one side, while the other simultaneously is given a similar one to the opposite side. This has been observed well in *Roccus*, *Epinephelus*, and a few others, but appears to be much more rare than the previous method. By a slight stretch, these might be thought of as anguilliform and ostraciiform respectively, and intermediates found, but it would seem to serve no useful purpose to so designate them or to create special terms for them at this time.

Pectoral propulsion: The pectoral fins in many fishes are used partly, and in some almost exclusively, for propulsive purposes. Such forms that have comparatively narrow pectorals used to this end, as *Abudefduf* and *Teuthus*, may be, in one sense, almost thought of as rowing their way along, in that they bring the fin forward almost edgewise and force it back broadside. However, a simple synchronous flapping of the pectorals produces a forward component similar to that of the ostraciiform tail. This is often seen in such broader finned forms as *Scarus* and *Tautoga*, and may be called the *labriform* movement. If such a pectoral be thought of as an ostraciiform tail moved forward, it is clear that its flapping would drive the fish forward and curve it to the opposite side. The other pectoral would deflect it oppositely and equally with the resultant reaction directly forward, as observed. The proof of this is that by turning the tail of the ostraciiform model so that it flaps against one side of the hull, thus approximating a pectoral of this sort, that end moves forward and curves as above described.

Other species, as *Spheroides*, undulate their pectorals in a manner similar to the way in which the tail is sometimes employed, as described under "Caudal undulation." In this case also these fins may be thought of as two forwardly displaced caudals whose angular divergence is complementary. This may be called the *diodontiform* movement. In actual practise, the movement is complicated by the fact that often the two above described methods are used simultaneously, combining the force of the first with the smoothness of the second, or an intermediate movement may obtain.

Many other minor movements are made by the pectorals of various fishes, but all have the preceding elements fundamentally. The following may serve as an illustration. *Cichlasoma* has been seen to produce a forward reaction by bending over both edges of the fin and beating them up and down together as indicated in Fig. 50. This causes two diagonal thrusts with a horizontal resultant.

Jet Propulsion.

That the force of the water exhaled from the gill orifices of fishes has a reactance which of necessity must be of some aid in

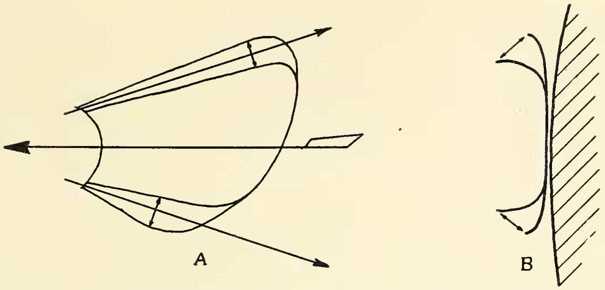

Fig. 50. Diagram of the pectoral movement as sometimes seen in *Cichlasoma*. A, side view. B, section. Both dorsal and ventral edges are turned over and beaten in unison producing divergent components with a forward resultant as indicated by the arrows.

sending them forward there can be no doubt. The amount of this force and its importance as a locomotor asset varies greatly, becoming large in certain forms and falling to nearly nothing in others. The underlying physical principles that are of advantage in placing slits in such a position as commonly seen has been applied to practical purposes by an engineer. These have been described by Breder (1924)[4], parts of which may be restated here as follows:

Mr. Clifford M. Paxton has invented and claimed patent rights on a strikingly novel method of propelling ships which he calls an "induced streamline system." The following brief consideration of this propulsion method is necessary to a proper understanding of some of these factors of fish propulsion.

The movement of a vessel is chiefly impeded by three obstacles, as described below:

(1) *Inertia resistance.* When a ship is propelled through the water all the submerged surfaces of the entrance section are subject to the adverse pressure of the relatively stationary water which has to be forced out of the way to make room for the advancing hull. This water is projected away from the ship and represents lost energy. As the ship moves, other water has to flow in by gravity to fill up the space the hull moves out of. At low speed this is not a serious matter, as the water is moved slowly and has ample opportunity to readjust its level by gravity flow. At higher speeds, however, this is not the case and the water is "pushed and piled up" in the form of a bow-wave about the entrance portion of the ship.

(2) *Cavitation.* Likewise, in reference to the after portion of the ship, water can not flow fast enough in response to gravity to fill in instantly the space vacated by the ship, and there result hollows or "low pressure areas" about the run or after portion of the hull. When a ship is propelled by the rearward pro-

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[4] This paper was the first published account of Mr. Paxton's invention.

jection of water from the stern the adverse effect of this cavetation is considerably increased. The rear low pressures augment the retarding effect of the high pressure created so that there results a pressure differential with a large rearward component, which is the dominant limiting factor in the speed of ships.

(3) *Skin Friction.* The frictional resistance between the ship's surface and the water through which it is forced, is not a limiting factor, and does not increase in the same ratio to speed as the pressure differential does; it is, nevertheless, an important item of resistance.

The first two of these resistance factors are as great or greater in the case of a fish, although the adverse pressures are not ordinarily visible as waves on the surface.

With an apparently simple but nevertheless very ingenious arrangement of "developed" jets, Mr. Paxton has greatly reduced the retarding effect of these factors and at the same time has been able to develop sufficient reactive thrust to overcome the remnants of resistance that still remain. The invention has progressed beyond the theoretical stage, so the inventor's actual model will be described in lieu of a necessarily longer exposition of the abstract principles. This model is nearly an exact reproduction of a modern destroyer, Class 186, reduced to an overall length of thirty-four and one-half feet on a scale of 1 to 9. On each side of the hull, midway between the waterline and the keel, a short distance aft of the bow a rearwardly directed nozzle is located, so placed as to cause water expelled therefrom to sheathe the under-water hull a short distance aft of them, this sheath completely surrounding the hull at midship. The position of the intake orifice is of slight importance, as long as it is always submerged, it usually being placed where most convenient and presented forward. At this point certain principles concerning the behavior of jets may be mentioned. Contrary to popular belief, the water set in motion surrounding a stationary submerged jet moves slowly in at right angles to the edge of the moving stream and then on contact passes along with it at a velocity only slightly inferior to that of the jet. This induced flow causes more water to move with it in a similar manner, and so on, thus spreading out the stream rapidly. The initial jet increases in sectional area by its deceleration, to which is added the constantly increasing induced flow. Paxton finds that with jets of high velocity the cumulative stream as thus built up may be more than a thousand times the cross section of the initial jet stream. The truth of the foregoing has been satisfactorily demonstrated by experiment.

Another fact to be here noted is that a stream ejected along the side of a curved form will follow the contour presented, even if the curve is convex to the axis of the stream, provided it is not too abrupt. The stream does not veer off at a tangent as might be supposed, but closely follows the bending of the curve. With these considerations in mind the manner in which Paxton overcomes the three obstacles to the speed of vessels by his method may be considered.

Through the nozzles described he pumps a small quantity of water at a high velocity and neutralizes the three impediments to progress, as will be shortly described. This system of propulsion is not to be confused with many which have appeared from time to time that were based on nozzle reaction and used a large volume of water at comparatively low velocity with the orifice located elsewhere. All such have been proven to be less efficient than the modern screw propeller. One important difference is that Paxton adjusts, within limits, the lengths of the pressure-reducing and pressure-increasing portions of the jet stream to the respective lengths of the bow and stern sections of the hull.

(1) *Inertia resistance.* This may be lowered slightly by a small amount of water passing into the propelling system through the intake orifice; but this is wholly inconsequential, since possibly less than one-half of one per cent of the water moved away from the high pressure region forward is taken into the ship. The discharge nozzle slits are so located as to be in advance of the maximum pressure region and by virtue of the water movement induced by the sheet discharged through these slits the bow-wave is in practice actually eliminated.

(2) *Cavitation.* The posterior depression is filled in part by the water ejected from the jets, but principally by the flow induced by them, so that the wake trends somewhat rearward instead of forward, and due to the water excavated from between the sheet jets and the hull it has a forward instead of a rearward component.

(3) *Skin Friction.* Considered as resistance to the ship's motion, this is largely overcome in that a considerable part of the frictional surface is transferred to the surface of the jet stream that sheathes the hull, for this may be considered practically as part of the vessel while it still follows the contour of it. There is an important addition to friction, however, on account of the high velocity streams being in contact with the hull.

The thrust of reaction of the jets on the nozzles is and must be equal to the remnant of resistance which remains after the net resistance reduction has been deducted. The reason for giving the jets a long narrow section instead of a circular one is for the purpose of placing a larger surface area in contact with the adjacent water and sheathing the hull satisfactorily; as well as concentrating the movement, reducing the time required for it, and adjusting the jet stream to the form of the hull. According to Paxton the modern screw propeller is more efficient than his new method at very low speeds, but at relatively high speeds the relationship is reversed.[5]

Returning to the fishes, it should now be obvious that the water ejected through the gill clefts of typical acanthopterygians is extremely similar in its effect to that of this new mechanical device that has actually propelled a model successfully. It seems, however, almost impossible to obtain an accurate measure of just what locomotor advantage this exhalation of water may be to most species, but it is readily demonstrated to be a real item in others.

Brugmans (1812) seems to have been the only naturalist hitherto to have considered the possible effect of exhalations and of course knew nothing of Paxton's factors.

An examination of over 300 diverse species of free swimming fishes taken at random (including both Teleosts and Elasmobranchs), most of which move at a considerable rate of speed, shows that over 90 per cent possess gill clefts at a place which Paxton pronounces to be the theoretically correct position for the most efficient use of this method, as far as he could tell from available material, considering the varying forms. The remainder consist of a few slight variations, none of which are large. Furthermore, even in sluggish forms the gill slits hold these positions fairly closely. It is only in such fishes as have progressed far from the typical ichthyized form that any wide variation is seen. Prominent among the latter are such highly specialized fishes as *Hippocampus*, *Histrio* and *Lophius*. In the fast moving forms long, narrow, gill clefts are found, as typified by *Seriola*, *Scomber* and *Pomatomus*, while in the more sluggish forms small and often nearly circular exhalant pores are present as in *Spheroides*, *Balistes* and *Lactophrys*. Practically all intergrades are found between the two extremes which are beautifully correlated with other locomotor structures and known habits. It is naturally difficult to obtain a measure of the force of exhalant water from living fishes moving at their higher rates of speed and at the lower rates perforce used in confinement, the body

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[5] All statements concerning his invention have been personally checked and approved as correct in a general way by Mr. Paxton, although naturally sketchy and inadequate for a full understanding of his invention as applied to ship propulsion. They are, however, sufficient for our purposes here.

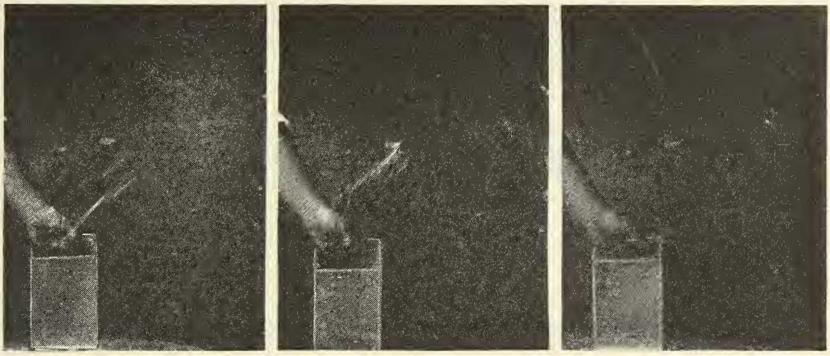

Fig. 51. *Chilomycterus schoepfii* ejecting water through the gill orifices while being held in the hand at the surface. A, the start of an exhalation. B, an exhalation in progress. Some drops that have reached a considerable height are falling at the right. C, the end of an exhalation with the last drops falling at the right. The jets have not been retouched in any way.

and fin movements which may be roughly analogized to a screw propeller have a great advantage. However, on the sluggish forms a definite demonstration of this force of the exhaled water is a simple matter, the Tetraodonts demonstrating it most clearly, although it must be admitted that here, on account of the rather wide divergence of the exhalant apertures, "nozzle reaction" plays a relatively larger part. Of these, *Chilomycterus schoepfii* shows its ability in this direction better than any others so far examined. It is simply necessary to hold an individual of this species with its mouth immersed to observe this. Having little flexibility of body, it is unable to squirm about and necessarily confines its attempts to escape to violently lashing the caudal, anal and ventral from side to side and waving the pectorals about in addition to squirting powerful jets of water through the gill orifices. In a fish six inches long these jets may attain a height of considerably over two feet above the surface of the water, (Fig. 51). That these jets are of great use in locomotion there can be no doubt. In fact, specimens of this species have been seen to impel themselves forward through the water by this means alone at not much less than top speed.

Other direct evidence was obtained as follows: A six-foot *Carcharias taurus* was permitted to swim in shallow water so that its back protruded. This caused a "bow wave" and a "posterior cavitation" to form as indicated by the solid line (Fig. 52). Every time the fish exhaled, the bow wave was considerably lowered and

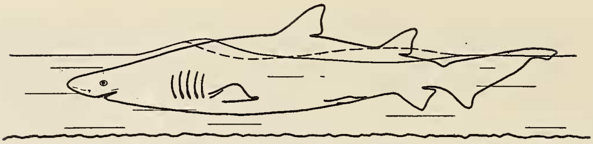

Fig. 52. *Carcharias taurus* swimming in shallow water. The solid line represents the bow wave and cavitation formed and the dotted line their reduction on each exhalation.

the cavitation more than filled as indicated by the dotted line in the same figure. On removing the pectorals of an *Abramis crycoleucas* it was found to be unable to rest without some forward motion unless touching some solid surface (Fig. 53) which shows the expedient it usually resorted to. More detailed evidence is given under the section "Maintaining a stationary position." As submerged jets of pure water are perfectly invisible, it is only when a suspended particle is acted upon by the jet that its force may be noted. Fishes that were held perfectly rigid so that there was no fin or body movement whatever appeared to be unable to eject jets with any force, simply respiring lightly, but as soon as the slightest tremor was permitted in the body the water was expelled violently. This suggests the possibility of a sympathetic nervous connection between the trunk and tail movements and respiration. Fishes of high speed, such as *Caranx* and *Seriola,* which could only be held with difficulty in a manner similar to that described for *Chilomycterus,* failed to respond appropriately, either flapping violently, or not respiring or if so only feebly, in such a manner that nothing could be deduced therefrom. The powerful *adductor operculi,* together with the branchiostegal rays and other compressible parts of the head, must make it possible for these species to eject water with a considerable velocity, and it may be mentioned that Paxton maintains that there is ample water ejected from fish held under such conditions to effect the purpose, the difficulty apparently being one of the velocity of ejection, which the musculature of the opercular and mandibular region could easily effect, were it not for some nervous inhibition incident to restraining the fish. Regarding the considerable strength with which fish can eject water through the mouth under experimental conditions, see Breder 1925 a. This is taken to indicate the great ejaculatory strength of the oral apparatus, the mandibular and opercular valves controlling only the place of the water's exit.

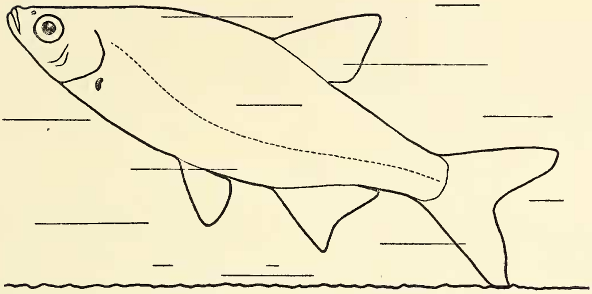

Fig. 53. *Abramis chrysoleucas* with pectorals removed. Illustrating the method by which the effect of the exhaled jets may be overcome, *i. e.* by dragging the caudal fin.

The reduction of skin friction is probably negligible in fishes on account of their effective mucous coat, but the other two and more important obstacles to speed must be overcome by muscular action.

Looking at the question from a phylogenetic standpoint there seems to be no very good reason why the port of exhalation in such diverse animals as elasmobranchs and teleosts should have such a community of placement, unless there is a positive advantage to be attained by so placing them or a definite disadvantage in having them placed anywhere else. This might be analogized to the necessarily similar streamline forms seen throughout fishes of high speed. If there was not some sound advantage in ejecting water forcibly it would seem a useless expenditure of energy on the part of many fishes while swimming to pump water in and out when by simply opening the mouth a greater amount would flow over the gill membranes as long as the fish moved forward, because the flow would not be intermittent. Actually, this has been observed in both *Carcharias taurus* and *Anisotremus surinamensis* when swimming leisurely. Furthermore, fishes which might be expected to make excellent use of this simplified manner of breathing, such as many members of the Carangidae and Scombridae, have a particularly well-developed opercular apparatus.

As the respiration of fishes, however, is an intermittent process it is clear that their mechanism would not be as efficient as a machine giving continuous flow. The exhalation of fishes is not to be confounded with the simple reactive jets of the so-called syringograde animals which suck up water slowly and expel it with violence through the same or a nearby aperture, such as the cephalopods, medusae and certain Odonata nymphs. This notoriously inefficient method may be compared to the discredited jet propulsion systems of the past.

Actions in a Current.

The preceding sections, for the sake of simplicity, deal only with forward motion through static bodies of water. If a fish, in progressing in any of the previously described manners, is in a straight flowing current instead of a still body of water, it is clear that in the main, the path traversed would be the resultant of the force and direction of the flow and that of the energy expended by the fish and its direction. However, a complication enters here which may modify the above somewhat, as the action of the current is dependent on the shape of the fins and body presented to it and their angle of presentation, as well as the eddy currents consequently produced. These generally tend to deflect a fish from its course and are considered under "Effects of current on maneuvering." In pursuing a straight line under such conditions, appropriate compensating acts are consequently required to offset these effects for, as the same angles are not always presented to the flow, due to the movements of the fish's body necessary to locomotion, the force of the current does not continually tend to press the fish in a single direction. Many fishes, however, will suffer themselves to be carried along by the current, especially if of a pelagic habit. In irregular currents, eddies, et cetera, straight line locomotion is more difficult and not infrequently impossible owing to the constant adjustments necessary to hold the course. This may be true even if the speed and force of the flowing water is comparatively slight, it being not simply a case of the fish's muscular efforts being overpowered.

Comparison, Interrelation and Discussion.

That the three primary methods employed by fishes to induce forward motion, (body movements, appendage movements, and respiration) are all advantageously interrelated is patent. In the majority of fishes, certain phases of each are present and are working harmoniously to the common end of driving the fish forward according to its requirements. No definite measure of the relative importance of each factor has been obtained for any given form although it can be said with little fear of contradiction that the metameral contractions of the lateral muscles are the most important to the majority of typical fishes, and that most frequently the other two are auxiliary. The appendage movements are especially brought into play for slow progression, and the respiratory jets (according to Paxton) for high speed travelling.

There appears to be no timing of the respiration to make it synchronize with the body movements, commonly several swings of the tail being made to one respiratory cycle. However the exhalation in fishes of carangiform locomotor tendencies seems to reach its maximum between flexures when the fish is straight forward, which would be clearly advantageous for mechanical reasons. In forms where jet and pectoral fin propulsion are found together, these fins are necessarily kept out of the way of the jets, for efficiency in straight forward swimming.

After having analyzed the various expressions of muscular energy directed toward propulsion, it may be well to consider the same from a synthetic point of view, for, after emphasizing the differences, it should be borne in mind how closely similar these different modes of propulsion are in reality.

First we considered the body undulations, split up in various ways for purposes of discussion, but actually representing only abbreviate or elongate expressions of the same thing. Secondly we considered the movements of the appendages, which are simply localizations of the same phenomenon and subject to the same gamut of elongation or abbreviation. Thirdly the effects of respiration were considered. It thus becomes evident that the means used by fishes to effect movement from place to place are among the most direct to be found anywhere and of great fundamental uniformity. The simplicity of "blowing" themselves along, coupled with the direct reaction of the primitive metameral lateral muscles, is not to be compared with the comparatively elaborate apparatus of the tetrapods. Even in the most highly specialized of fishes the same elemental movements are to be found, hardly beclouded by the extreme specializations under which they operate.

The great expression of undulation, reciprocation and wave motion throughout the swimming of fishes brings to mind Spencer's "Synthetic Philosophy" (1892) and his views of the general signif-

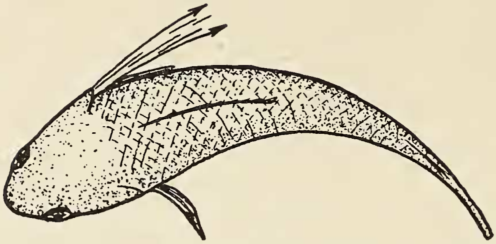

Fig. 54. Diagram of a fish turning by several methods. Myomeres on one side contracted, pectoral fin held out, tail held to one side and exhalation through only one gill orifice.

icance of undulation. The philosophic concept of artists, which regards a circle as indicative of place and a straight line as indicative of direction and a sine curve (their combination) as indicating motion, also would seem to find expression in the swimming of fishes.

MANEUVERING.

In general, maneuvering in fishes consists largely of differential application of the locomotor efforts which would otherwise produce forward motion, together with a variety of special acts, most of which are limited to certain forms, rather than being generally applied.

Turning.

Turns may be made while moving forward by any of the following means:

Body movements.

(1) Metameral waves may be propagated in greater number or be of larger size on one side than the other, instead of simply alternating uniformly.

(2) Several myomeres on one side may be held tightly contracted so as to hold the body flexed while some other effort drives the fish forward (Fig. 54).

Fin movements.

(1) A pectoral fin may be held out at an appropriate angle to the body. The further forward the fin is thrust the sharper will be the turn (Fig. 54).

(2) The tail may be held rigidly to one side, acting like a rudder (Fig. 54). This usually accompanies "2" of "Body movements," as a posterior continuation.

(3) The dorsal and anal may be held over to one side.

(4) Fishes using pectoral propulsion may cease the operation of one fin while the other continues as before.

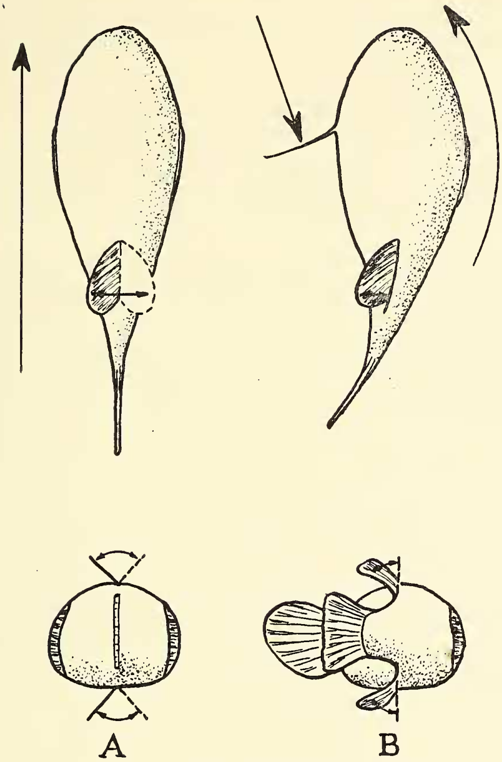

Fig. 55. Diagram of a tetraodont such as *Lagocephalus* turning by several methods. Dorsal and posterior views. A, straight line swimming. (Tetraodontiform.) B, turning to the left. Pectoral extended, caudal held to one side and dorsal and anal oscillated one side.

(5) Fishes using a simple flapping movement of the dorsal and anal may oscillate them both over to one side (Fig. 55).

Respiratory action.

(1) The operculum of one side may be held down tightly, forcing all the water out through the opposite one. The gill cleft on the outside more or less automatically opens and the inside one closes if the body is flexed to any great extent because of its bending away from the head on the convex side (Fig. 54).

These comprise the movements on which turning depends when swimming actively. The side to which the turn is made is obvious and needs no elaboration. Usually more than one method is used at a time and in such sharp turns as is seen in *Salmo* after having risen to a fly it is likely that as many as possible are used in combination. Fishes which wheel about in great circular paths often use a pectoral alone. *Lagocephalus* and others may turn very abruptly by backing with one pectoral and oppositely moving the other, with all vertical fins "hard over." Schlesinger (1911, b) points out with a diagram that in turning by means of extending a single pectoral the pressure of the water on the extended dorsal and anal swings the fish around with the pectoral somewhat as a pivot. This is especially noticeable in long bodied forms, such as *Esox.*

Fishes at rest may face about without perceptibly moving forward by opposite fin movements on either side of the body. That is, such pectoral fin movements mentioned above for *Lagocephalus* will practically turn the fish on a point if no forward motion is being made. In such long bodied forms as *Esox* and *Lepisosteus,* the pelvics may be brought into play also to aid in this action. Many methods are thus employed by various species.

Probably the most common method is a single flap of the tail to one side. While this, of course, gives the fish some forward motion, the pectorals are frequently held out as breaks so that no long glide results. In this action the tail is expanded to its full extent in making the stroke and contracted on its return to the median position in order to prevent a reverse turning action or any more forward motion than necessary.

Rising and Falling.

In rising and falling both fin movements and hydrostatic elements enter, the former as direct acts and the latter rather passively.

Fin Movements: As an appropriate movement of the pectorals can deflect a moving fish from a straight line to the right or left so may they by proper twisting cause it to move diagonally upwards or downwards as diagrammed (Fig. 56). This method is effective only if the fish is actively swimming as the fins are held passively up or down, their position as planes, and not any motion of theirs, determining the course taken. The resultant is the product of the inclination of the plane and the horizontal thrust. Fishes not actively swimming may use the pectorals somewhat as active paddles and obtain a similar result by twisting them appropriately and employing methods described under "Pectoral propulsion." In the case of fishes whose undulations are in the vertical plane as

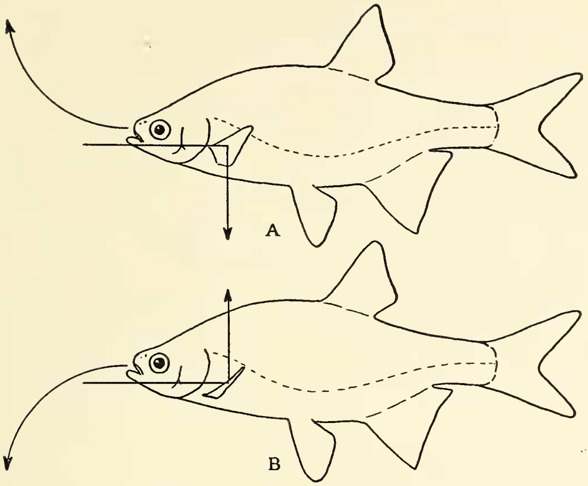

Fig. 56. Pectoral control of elevation. A, pectoral turned to effect an upward movement. B, pectoral turned to effect a downward movement. The angled arrows indicate the manner of impingement of the fins. The curved arrows indicate the directions of travel.

with skates and flounders, certain of the methods of body undulation used for turning in other fishes cause ascent or descent.

If a temporary tendency to rise or fall is not desirable and not readily obviated by the hydrostatic apparatus, the fins may be used to offset it and maintain a definite horizontal plane until an adjustment is made, by using any of the various muscular efforts, that will effect the desired result.

Hydrostatic Elements: In most fishes lacking a swim bladder, the specific gravity is slightly greater than that of the waters they inhabit, and immediate although generally slow sinking follows on a cessation of active swimming. In some forms this may be greatly retarded by the expansion of a large horizontal surface as in the case of the triglids with their long plane-like pectorals (heavy although possessing a swim bladder). Others are so close to the specific gravity of the waters they inhabit, due to the presence of sufficient fat, that only the slightest movement suffices to keep them from sinking or rising, as in the case of *Poronotus*. Prominent among the various fishes lacking a swim bladder may be mentioned Cyclostomata, most Selachii, Scopelidae, *Scomber scombrus*, *Menticirrhus*, Alepocephalidae, Cyclopteridae, and Pleuronectidae. Both free swimming and bottom dwelling forms are here represented.

This lack of a swim bladder in other than bottom forms is found only in marine fishes, the quantity of fat or other buoyant substance necessary to float a fish in the less dense fresh water being practically prohibitive as suggested by the work of Taylor (1922). Obviously any fish permanently or temporarily heavier than water may descend at will in any direction and at nearly any gradient by inclining their fins appropriately, depending on their structures. This is very commonly seen in the triglids although nearly all fishes of high specific gravity appear to use it at times.

The vast majority of fishes, however, possess a definite hydrostatic organ, the swim bladder. Much controversy has centered about this organ for in many forms it is undoubtedly used for numerous other purposes, such as a means for sound production or as an auxiliary breathing apparatus. The fact remains, however, that it must of necessity affect the flotation of the possessor. It has been proven to be adjustable to various depths as Du Bois-Reymond (1914) points out and makes a stationary position, with regard to vertical movement, readily possible within certain limits of depth. Various methods by which the gas in the swim bladder is probably controlled have been suggested from time to time and the probability is that nearly all have some truth in them.

Although a detailed discussion of the action of the swim bladder is not within the province of the present paper, the following brief consideration may be given it. Even if the bladder be considered as a passive reservoir, the pressure of the superimposed column of water above would tend to compress it to a certain extent, proportional to the depth, but as it is well protected by its place in the fish's body, this effect is probably comparatively slight. In accordance with this is Du Bois-Reymond's corollary that a fish with a specific gravity of unity at a given point will descend with increasing rapidity if once started, on account of the slight compressibility of water and the rapidly increasing superimposed weight of water (one gram per sq. cm. for each cm. of depth) causing compression of the gas and a consequent increasing specific gravity differential. The opposite is the case in rising. It is conceivable that voluntary muscular control of the size of this organ and consequent variation in the bulk of its contents might be used by some species to cause a rising or falling of the fish. In changes of considerable depth the secretion or reabsorption of gas by the blood no doubt plays a prominent part in stabilizing the animal and moreover is acting reflectively at all times with the purpose of keeping the fish at the desired depth. That these various factors are always working to maintain the proper specific gravity is clear if it be considered that in the normal life-processes of food taking, digestion and excretion, the bulk of any fish is practically incessantly changing slightly, and small adjustments must be made continually.

The following experiments demonstrate that in *Fundulus heteroclitus* and *majalis*, at least, both of which possess well developed swim bladders, the adjustment in flotation to different densities is not instantaneous.

One dozen of each species was transferred as follows from salt to fresh-water and vice versa:

TABLE II

Exp. No.	*Transferred from*	*Transferred to*	*Result*
1	Salt water sp.g. 1.024	Fresh water sp.g. 1.000	Sank
2	Fresh water sp.g. 1.000	Salt water sp.g. 1.024	Rose
3	(No. 1 back to salt water)		Rose slightly.
4	(No. 2 back to fresh water)		Sank slightly.

From this table it is evident that the reactions are the result of an adjustment that is not immediate. In Nos. 1 and 2, all the specimens occupied the bottom and top halves of the jars respectively, and it was clear from the pectoral movements that in the first case these were directed to drive them upward and in the second downward. In between five and ten minutes, they began to distribute themselves more equitably, but there was still a slight difference between the two jars. By fifteen minutes, the two sets were indistinguishable. On transferring back (No. 3 and 4) a similar lack of immediate adjustment was evident, but not nearly so great, from which it is judged that the first adjustment was not as complete as it first appeared.

Starting and Stopping.

In starting ordinarily the movements of swimming are simply initiated, as pointed out under descriptions of the various types of locomotor efforts. However, the pectorals, usually held out from the body when resting, are quickly brought back flush with the body and remain there except in the pectoral type of locomotion. A violent exhalation may be made at the same time also. These actions, of course, give an added impetus to the initial effort.

Fishes may come to a stop gradually by simply ceasing to operate the locomotor musculature, in which case they glide for a

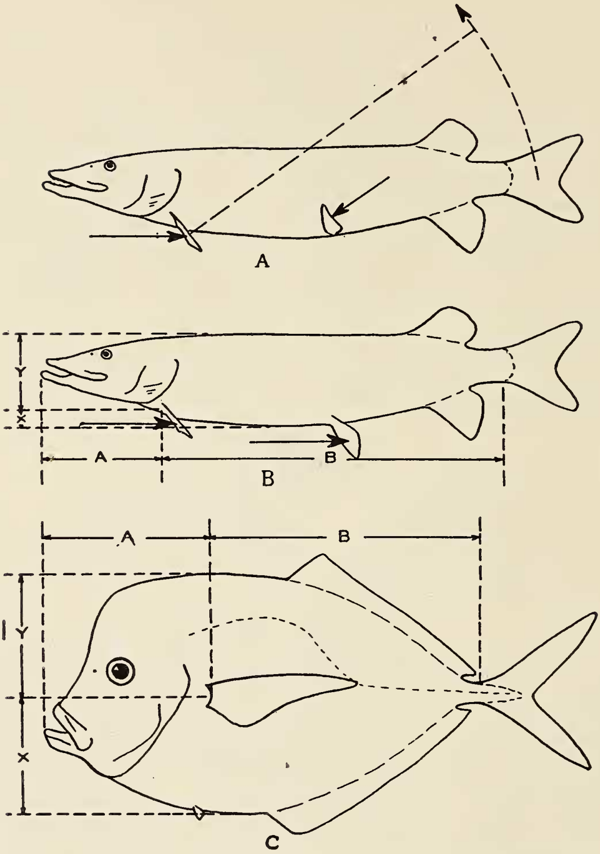

Fig. 57. The effect of the relative positions of the fins on stopping. A, manner in which the hind end of *Esox* rises if pectorals only are used as brakes, unless checked by the pelvics as shown. B, manner in which an abrupt stop is made by *Esox* with both pectorals and pelvics used as brakes. Note that approximately A : B : : X : Y. C, Comparison with *Vomer*. Note that here too approximately A : B : : X : Y, but the pectoral is much nearer to a central location, obviating the necessity for the large posteriorly placed pelvics.

considerable distance before coming to absolute rest. Most frequently, however, they employ some muscular activity to neutralize the no longer desirable motion initiated by other contractions of muscle fibers. Anguilliform fishes may suddenly reverse the direction of the motion of the undulations and by this means quickly check forward movement or they may suddenly hold themselves rigid in any position and check the motion more gradually. Fishes with such undulations localized in the fins accomplish the same result with their particular locomotor structures in a similar way. This can be readily observed in *Amiatus* and *Gymnotus,* but *Raja* seems never to employ a reverse movement although it may rigidify itself. All fishes which have been noted to reverse their primary locomotor "gear" have also been noted to deliberately travel, at least short distances, backward by this means. *Gymnotus* and related genera are the most expert in this performance of any of the forms studied. There are good mechanical reasons why *Raja* could not do it very effectively, judging from its shape.

Fishes of a carangiform tendency in locomotion are not known to show a reversal of the primary locomotor movements, the pectorals playing an important part instead. These are usually stuck out equally on both sides, thus forming an effective resistance to forward movement. In such long bodied forms as *Esox* it is clear that if the low hung pectorals were simply dropped, while they would stop the fish, they would likewise "trip it up," *i. e.,* cause the caudal portion to raise up because the point of pressure is anterior and low (Fig. 57 A). In order to avoid this the pelvics which in these forms are placed well aft are held as indicated in the figure which, because of the close similarity in size and shape of the two sets of fins, counteract the tendency of the tail to rise. This expedient is resorted to in an attempt to make a slow stop. If an abrupt stop is desired both pectorals and pelvics are thrown down simultaneously at approximately the same angle, thus producing two points of resistance, one forward and the other aft, which causes no tendency for either end to raise. (Fig. 57 B).

In short bodied fishes this tendency to tip up is materially lessened on account of their short fore and aft dimension and a corollary to this is the fact that the pectorals are closer to the middle of the body, from front to back as well as from top to bottom (Fig. 57 C). With this may come a reduction of the pelvics as in *Vomer,* or the pelvics may remain large as in *Lepomis.* The former condition is found typically in forms which swim continuously for long periods, as pelagic fishes, *e. g. Poronotus,* while the latter condition is typical of lacustrine, fluvitile and reef fishes which habitually stop frequently in their locomotor efforts, *e. g. Lepomis, Chaetodipterus* and *Pomacanthus.* Roughly, the tendency connected with a shortening, deepening and narrowing of the body is for the pectorals to become more nearly centrally located, antero-

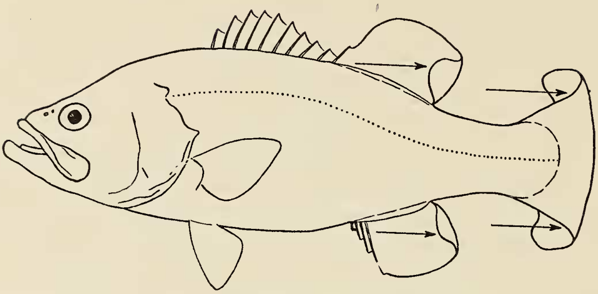

Fig. 58. *Micropterus* with the dorsal and anal lobes curved to one side and the caudal to the other so as to form a "sea anchor."

posteriorly and dorso-ventrally, while with a lengthening and widening of the body the pectorals tend to move forward and downward and the pelvics backward and downward and to approach them in size. Generally speaking, approximately A : B :: X : Y (Fig. 57 B and C). As in nearly all of the modifications mentioned in this paper, a complete series of variations is found grading from one extreme to the other.

Acanthopterygians that have the bases of the pectorals and pelvics usually placed rather close together and are comparatively long bodied also usually have the tips of the dorsal and anal lobate. These are frequently brought "hard over" to check movement. The genera *Micropterus*, *Epinephelus* and *Micteroperca* quite commonly employ the tail in this manner, virtually forming a sea anchor. Any tendency caused by this to bring about undesirable deflection to one side is counterbalanced by an appropriate pectoral movement. *Lepomis* and *Micropterus* at times curve their tails to one side and the dorsal and anal lobes to the other, thus checking movement and avoiding deflection (Fig. 58).

As many fishes may eject water through the mouth, it follows that there is some slight reactive effect which probably in most cases, however, is negligible and rarely used. The only direct evidence we have of its effect is that to be noted by watching *Balistes*. This genus, especially *B. carolinensis*, with its mouth a few inches away from sandy bottoms will repeatedly blow water out excavating a small hole in the sand in its search for small worms and other burrowing forms, habitually seeking food in this manner (Breder 1925 a). The force of this jet, directed against the bottom is indicated by the way the fish braces its pectorals, undulates its dorsal and anal and so on, although even then, at times, a slight backward recoil is noticeable.

In stopping, the dorsal and anal of most spiny rayed fishes are usually erected to their fullest extent. That these fins are chiefly concerned with the maintenance of an even keel may be proved by the removal of them. Fishes of this type so deprived are able to swim practically as fast as before, but roll slightly from side to side with each half cycle of undulation, especially when starting or coming to a stop. Once well under way, this twisting largely disappears. Rapidity of motion continuously made, without acceleration or deceleration and absolute rest obviates to a certain extent the necessity of these keels which are then ordinarily folded back. See under "Reomorphism." The pelvic fins further this same maintenance of position by functioning after the manner of bilge keels. This is especially prominent in many of the sharks with the long and evenly outstanding pelvics.

Maintaining a Stationary Position.

The maintenance of stationary position is by no means a simple matter with fishes which do not merely rest on the bottom or hold fast to some object by means of prehensile or suctorial specialization. Allowing the hydrostatic apparatus to be perfectly adjusted so that there is no tendency to rise or fall, which condition is frequently approached, and that the fish is in perfectly still water there are still other factors to be reckoned with.

It has been argued by Osburn (1906) and others that the continuous movements of the paired fins while a fish is at rest are for the purpose of maintaining equilibrium. The experiments of Osburn were performed on *Fundulus heteroclitus* from which he claimed to have found the following:

> ". . . When a single pectoral fin was removed the fish tended to turn partly on one side, due probably to the action of the pectoral of the opposite side. This, however, the fish soon learned to regulate. After the removal of both pectorals the fish when swimming slowly apparently moved as usual, but when forced to turn quickly it was unable to accurately balance or otherwise undergo movements requiring nice adjustment. . . . A study of the movements of many species of fishes in the New York Aquarium is entirely confirmatory of the view that one function of the pectoral is to balance and accurately adjust the fish in swimming.
>
> . . . Fishes with the pectorals removed would at first frequently run

against the side or bottom of the tank, but later they learned to avoid this by a strong movement of the tail.

. . . , it is a point of observation without a single exception in my experience that the ordinary, actively swimming type of fish when resting on the bottom does not move the fins at all.

. . . On the other hand, all fishes that I have observed use the pectorals when they are suspended in the water. Moreover, other fins are often brought into use at the same time. Thus the elongate pike (*Lucius*) and gar (*Lepisosteus*) are seen to move the pelvic fins slowly, coordinately with the pectorals, and short bodied forms such as the butterfly fish (*Chaetodon*) move the pectorals and caudal, while in species intermediate in form the caudal, anal and dorsal may, any or all, be used in addition to the paired fins when suspended in the water. This array of facts makes it quite clear that the function of the pectorals when the fish is stationary is that of equilibration and not the removal of water charged with carbon dioxide."

This latter statement refers to Duges (1905) who contended that the motion of the fins was to cause a current supplying fresh and removing vitiated water from the gill region. How the fish managed to remain in a stationary position if freely suspended while doing this appeared not to concern him. Osburn summarized the functions of the pectorals as follows:

> "Guiding and balancing the body in swimming;
> To act as a brake in arresting the progress;
> Equilibration when suspended stationary in the water and
> Locomotion, either forward or backward."

While Osburn's work is here accepted in general, it is objected that the balancing and equilibrating function upon which he places so much stress is of minor importance and almost negligible as the subsequent evidence will serve to indicate.

In spite of the various functions ascribed by other students[6] to the movements of the fins while at rest, ranging from that of supplying new water to the gills to the more rational one quoted in part above the following is offered in substitution.

Fishes in respiring eject water through their gill orifices in a backward direction as pointed out under "Jet propulsion." It is axiomatic to state that if a jet of any sort whatsoever be ejected at a velocity however low from a body freely suspended, there will be a proportional reaction in the opposite direction. Therefore, if a fish is not to move forward at a speed dependent upon the rate

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[6] Since this manuscript has been prepared, a paper "On the Functions of the Fins of Fishes" Schmalhausen (1916) has been received. It is in essential agreement with the conclusions presented here and discusses certain factors in more elaborate detail accompanied by six interesting diagrams. The effects of respiration are not considered.

and force of respiration when resting, some counteracting effort must be made. The following is given in support of this view and is taken in part from Breder (1924).

Over a dozen diverse species were experimented upon by the removal of some or all of the fins; the species including those used by Osburn and others and varying in form from such extremes as the log shaped *Esox reticulatus* to the deep, thin bodied *Vomer setapinnis*. The results obtained were an embarrassment of movement, depending on what fins or combinations of fins were removed, but in *no* case was a distinct disturbance of equilibrium obtained. As long as the individuals remained at rest and attempted no turning or other maneuvering they retained the *normal* horizontal position. The present experiments demonstrate that the stability of the equilibrium of fishes is not controlled by fin action, general statements notwithstanding. True, dead or very sick fish often float belly or side up, but this is no doubt attributable to other more or less obscure physiological causes: derangement of the digestive tract, lack of control of the gases of the swim bladder, et cetera.

The centers of gravity of numerous free swimming species were found to fall within the air bladder. This was found by balancing them in two planes on a knife edge.[7] Various comparisons made in and out of water showed that taken as a whole these fishes could be considered as being of virtually uniform specific gravity, even though constructed of many different and diverse substances. This is not in accord with the generally accepted belief that fishes are in an unstable equilibrium normally, which view has been based on injured or diseased examples and their clearly unstable equilibrium. Fig. 59 illustrates the position of the center of gravity with reference to the swim bladder in four species. An inspection of this will show that if the body be considered as of uniform specific gravity, the center of gravity of the entire fish and that of the swim bladder itself practically coincide. This clearly makes for an ease of motion from side to side as there is no great pendulum action to rapidly erect (or turn over) a fish, and partly explains the ease with which certain labrids, scarids, and others swim on their sides at times. Mr. E. C. Bennett points out in this connection that it is his belief that the center of gravity and the center of buoyancy would be found to coincide in most fishes.

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[7] See Appendix, page 293 for a description of the apparatus used in this connection.

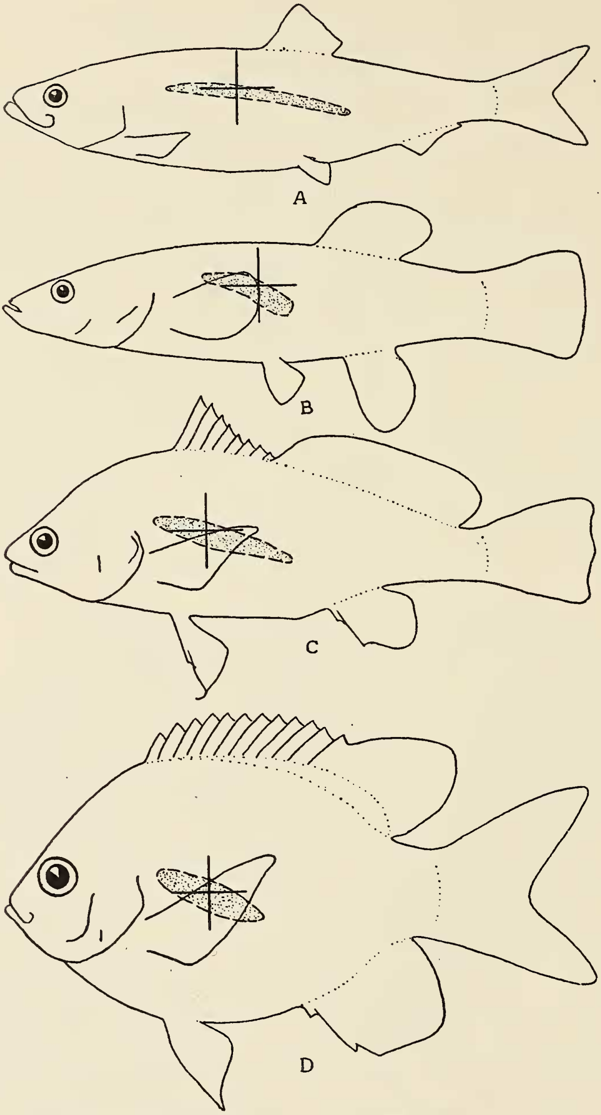

Fig. 59. Location of the center of gravity in fishes. The cross lines indicate the position of the center of gravity. The shaded area indicates the position of the swim bladder. A, *Clupea harengus.* B, *Fundulus majalis.* C, *Aplodinotus grunniens.* D, *Eupomcentrus leucostictus.*

A superficial glance at nearly any typical fish poised quietly in the water should convince anyone that the pectorals are engaged in backing water. That is, the effective thrust is forward, which would tend to move the specimen in a backward direction, or just the reverse of what is described under "Pectoral propulsion." However in connection with the effect of the exhaled water it is conceived that the function of this movement of the pectorals is to neutralize its reactive force. This backwardly moving intermittent stream of respiration is not to be understood, however, to have any considerable force, while the fish is at rest, as naturally the respiration is slower and furthermore the gill clefts are observedly opened wider at such times, thus reducing the velocity of the emerging streams as well as increasing the cross-sectional area of them and consequently reducing both their velocity and surface area per unit of volume. The pectorals being usually placed directly behind the gills are enabled to intercept the stream and check the original direction of the thrust. The truth of these assertions is by no means simple to demonstrate, owing to the large number of locomotor organs that generalized fishes employ either singly or in numerous combinations. In fact, it is rather seldom that fishes are seen free in the water with no apparent motion other than the pectorals. At such times they are seen to back water rhythmically and usually in perfect synchronism with the respiratory movements. That is, as the pectorals come forward the operculum lowers and forces the vitiated water out, the inhalation accompanying the return stroke. Usually, however, there are some other movements such as undulation of the dorsal or caudal as well as various others which complicate matters so that it is a matter of patient waiting for a proper opportunity to see these two factors working together alone in direct opposition to each other. The significance of these other motions is treated under the heading "Relationship to habits and development." In very cold water when *Chaenobryttus* is in a state of semi-hibernation they may sometimes be observed with no fin movement at all and with both sets of paired fins securely pressed against the sides. At such times the respiration is extremely superficial and appears to have little reactive effect. However, after a long period of time it was observed that they do move forward ever so slightly and that very occasionally the pectorals are brought into play to regain the previous position. However, they generally allow themselves to come in contact with some piece

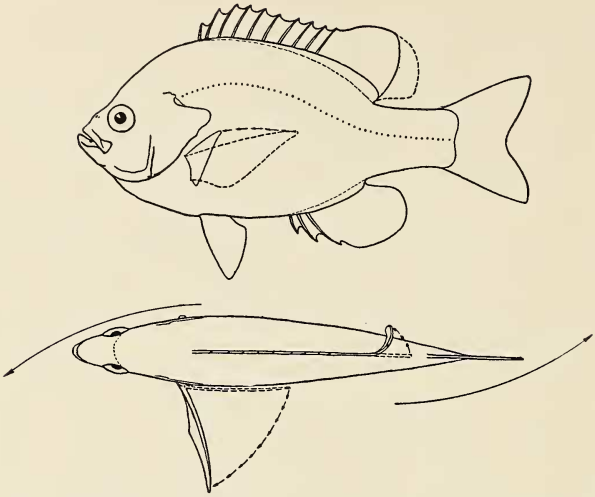

Fig. 60. Diagram of the behavior of a Centrarchid (*Lepomis pallidus*) minus one pectoral. In attempting to maintain a stationary position the backing of the pectoral was insufficient and the fish curved forward toward that side. An increased pectoral action caused it to curve backward to the opposite side. Later the dorsal lobe was brought into play and a stationary position was maintained.

of brush or other object in which case the friction is sufficient to stop motion. The removal of a single pectoral from a specimen of *Lepomis pallidus* demonstrated this still further. On composure after release it backed water as usual with the remaining pectoral fin but as the force applied was only one-half of that previously used and on one side only, the fish moved forward, slowly curving toward the side possessing the fin. This motion appeared to disturb the specimen, causing it to speed up the number of oscillations. As now the force of the fin overcame that of the jets the fish moved slowly backward and curved slightly to the opposite side. In a short time the fish learned to compensate for the missing member by waving the posterior tip of the soft dorsal which it bent towards the side of the missing pectoral, and from then on had no difficulty in maintaining any position desired (Fig. 60). Most of the Centrarchidae use either or both median fins in this manner occasionally, making the learning of this accomplishment no new feat. On this account it is usually done by specimens practically immediately on coming to rest, the particular individual mentioned above probably representing a slight abnormality in nervous adjustment.

The removal of fins from *Fundulus heteroclitus* yielded the

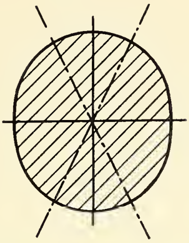

Fig. 61. Cross-section of *Fundulus heteroclitus*, indicating maximum roll of finless examples. The solid lines indicate the normal horizontal and vertical axes. The dot and dash lines indicate the extreme angular displacements of the vertical one.

following results. Compare with those of Osburn quoted on pages 209 and 210. These observations are given with reference to equilibrium only, as at no time were the specimens sufficiently quiet to observe the effect of their exhalations.

One pectoral removed.—Very slightly inconvenienced, movement almost as in the normal fish. Turns toward the side of the missing member were made with difficulty.

Two pectorals removed.—A slight tendency to roll while swimming straight ahead was noticeable. Any turning difficult.

One pelvic removed.—Even less inconvenience experienced than with the removal of one pectoral.

Two pelvics removed.—A slight tendency to roll was noticed, but much less than with both pectorals missing.

One pectoral and one pelvic (same side) removed.—A slight tendency to roll was again noticeable. Turns were negotiated with difficulty as were changes in level.

Two pectorals and one pelvic removed.—A greater tendency to roll was noticed. On release the fish dove to the bottom and at first had considerable difficulty in rising.

The following day all were up and active having accommodated themselves to their various handicaps. Fig. 61 shows in cross section the greatest amount of angular swing noted in any. This could be hardly construed as a turning "belly side upwards" as mentioned by Bridge in the Cambridge Natural History (1904). Further, this diagram is somewhat exaggerated, and the rolling became progressively less as the specimens became adapted to circumstances and learned better to control themselves with dexterous twists of the remaining appendages.

Further experiments on other species are given below:

Lepomis pallidus.—One pectoral and one pelvic (same side) removed. The action was indistinguishable from that described previously with a single pectoral missing.

Two pectorals removed. This fish failed to stop forward motion except when resting with the pelvics in contact with something, rolled slightly in swimming and could not turn well.

Two pelvics removed. Did not stop as abruptly as a normal fish. Not inconvenienced while at rest unless in a slight current, when a wabbling motion was noticeable.

Abramis chrysoleucas.—Two pectorals removed. Could not stop forward motion except by dragging the tail along the bottom, thus resting in a diagonal position. See Fig. 53.

Two pelvics removed. Only very slightly inconvenienced in turning and stopping.

Esox reticulatus.—Two pectorals and two pelvics removed. Swam and turned more awkwardly than a normal fish. Bent dorsal and anal and so maneuvered while nearly at rest. Rose and fell fairly well.

Two pectorals, two pelvics, dorsal and anal removed. Swam with difficulty. The median fins seem to have a distinct propulsive function, being placed so far aft and automatically sharing in the oscillation of the body, as pointed out by Schlesinger (1909). Maneuvering power greatly restricted. Did not remain perfectly still as is their habit.

Lagodon rhomboides and *Eupomotis gibbosus.*—One pectoral removed. Dorsal lobe bent around and compensated generally at once.

Vomer setipinnis.—Two pectorals removed. Unusually little inconvenience noted. In a tank of normal examples it could not be distinguished for any abnormal behavior, although this species constantly waves its pectorals about.

Scardineus erythropthalmus.—Pectorals held down tightly to body and operculums held closed by a band of very thin rubber. Short stops not made successfully, the ventrals being insufficient brakes. Turning not so gracefully or accurately done.

Effects of Current on Maneuvering.

Maneuvering in a current has much greater complication than straight forward swimming under such circumstances. That is, a current may generally either help or hinder maneuvering in a more marked manner than it does rectilinear locomotion.

Turning, rising and falling are affected either advantageously or adversely depending on the angle of the flow in relation to the direction of the changing axis of progression. That is, in a turn produced by any of the aforesaid methods the current may so impinge on the curves of the body, the projecting fins etc., as to hasten the turn or retard it. This, of course, is also true of altitudinal changes.

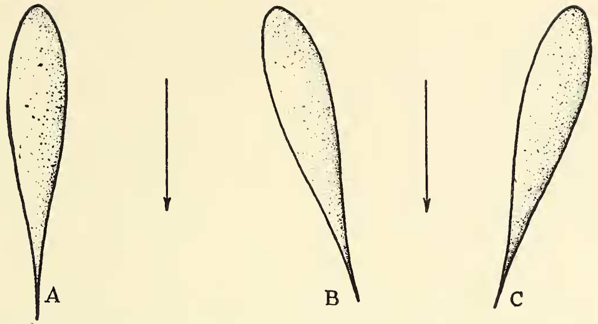

Fig. 62. Maneuvering in a current. The direction of flow is indicated by the arrows. A, normal mean position in swimming actively against a current. B, and C, either side of a carangiform oscillation from which active swimming is started to regain a lost position.

Starting, stopping and the maintenance of a stationary position is somewhat more complicated however, and may be considered briefly below. In holding a position in a current, fishes head up stream as this minimizes the frictional resistance of the flow against their bodies by reason of their streamline shape; and in this position they are properly orientated for swimming against it. Here the effect of respiration aids in holding their position and need not further be considered in this connection. A nearly stationary position may be held simply by actively swimming against the current just fast enough to balance the effect of the water in carrying the fish down stream, *i. e.* by swimming just as fast in one direction as the water flows in the opposite. This method may be observed in a fish culturist's trough of salmonid fingerlings.

A fish so maintaining a stationary position in a current may desire to drop back to a position further down stream. This is generally done, not by turning, but by simply stopping the swimming movements and drifting passively back. The drifting back is generally not done in a position with the body axis parallel to the current, but at an angle to it equal to the amplitude of the propulsive contortions (Fig. 62), in which A represents the mean position, parallel to the direction of flow, and B and C the fish at either side of an oscillation (similar to A and C of Fig. 44). These latter two are the positions held for drifting down stream. Starting from one of these, as is frequently done to regain the original position, the fish is already in the best possible position to initiate motion against the stream flow, instead of having to make that first flexure from the less effectual position directly in line with the flow. See under "Body movements." In the ordinary distances so drifted there appears to be very little change of this angle due to the action of the current. The speed that a fish facing a current can sometimes attain is surprising, as its actual motion is, of course, the sum of its observed travel plus that of the stream flow. See Stringham (1924).

Comparison, Interrelation and Discussion.

It should now be evident that all the various elements that go to make forward progression possible are likewise involved in maneuvering, together with numerous others not directly concerned with straight line locomotion. The "propelling devices" and the "steering mechanisms" are so inseparable that it is generally impossible to say where one leaves off and the other commences. Maneuvering in the main is effected by differential applications of the motor system generally; body movements, fin movements and exhalations, all being capable of use in maneuvering as well as in driving the fish forward. However, in more generalized fishes the metameral muscles of the trunk may be roughly compared to the driving engine and the appendages to the steering apparatus, in a very broad sense.

The innumerable interrelations of the many factors concerned with orientation and nicety of movement makes the isolation and description of any one of them particularly difficult for it is seldom indeed that one is to be seen operating alone. The removal of members while giving collateral evidence is not completely satisfactory in itself. Observation of many individuals of varied species under normal and abnormal physical conditions acting in a manner slow enough for the eye to follow has been found in many cases, after much experimentation to furnish the most reliable data, when studied with the axioms listed on page 165 in mind.

MOVEMENTS OTHER THAN SWIMMING.

Nearly all fishes are primarily adapted to locomotion while freely suspended in water and all factors treated under the present head may be considered as secondary adaptations to special environments and habits.

Burrowing.

One of the common habits of many fishes not properly to be considered as swimming is burrowing. This is generally associated with the strict anguilliform type, but not necessarily, *e. g.* many labrids, such as *Iridio*, are capable burrowers. Burrowing is generally effected by an active swimming with the nose pointed into the sand. This is continued until a sufficient length is covered to allow the various muscular contractions to obtain a grip on the sand, after which progress is more rapid, the tail portion then frequently trailing into the burrow passively. Other forms such as skates and flounders generally throw the sand over themselves, not burrowing in the sense described above, while still others employ somewhat intermediate methods.

Creeping.

Many various groups are modified for motion along a solid surface, generally only in a nearly horizontal plane. The triglids, for example, are able to creep slowly over the bottom by means of the free pectoral rays. The motion is produced by placing the tips of the rays in contact with the bottom and pushing backwards. This movement may be simulated by running the hand over a table top with three finger tips touching it and moving somewhat as legs. There seems to be no especial sequence in which the rays are used. Fishes with a suctorial disc such as the Petromyzontes, Gobioformes and Loricariidae, all seem to be able to adhere to any surface almost independently of its angle of inclination, providing it is of the proper texture. By slight movements of these discs they can inch their way along slowly for short distances, in various degrees of effectiveness depending on the structure of the disc. Flounders may push themselves forward by means of the fringing rays and skates can kick back with their modified ventral fins. See "Part II—Systematic" for further details of this sort.

Anguilliform fishes of nearly cylindrical cross section can move over solid surfaces out of water by applying their particular locomotor movements. In such a case the contact with the supporting surface is the only place of effective pressure, the air being so tenuous as to be entirely ineffective as a resisting medium to these movements. Therefore the oscillations are of wider amplitude, as it is natural that they would be and indeed need to be, for this manner of movement is very inefficient. Advantages not dissimilar to those to be had in the case of burrowing are found with eels moving through grass or over rocky places on account of the increased contacts.

A fish of carangiform locomotor apparatus out of water flops from side to side because in contracting the myomeres of one side as it normally does, the tail hits down smartly and the reaction throws the fish upward.

Incidentally in this connection experiments were made upon *Fundulus heteroclitus* in an effort to determine whether they could direct their flipping movements out of water and so find their way seaward if left stranded on a beach as is claimed, Mast (1915). The results of the present experiments were as follows: If the surface (in full view of and near to open water) is perfectly smooth and level, the fish simply hop up and down "progressing" indifferently in any direction and often coming back to the same point. If it is slightly tipped in any direction, the vast majority move down the incline as would be expected for mechanical reasons. Similarly if a strong wind is blowing they tend to move with it. If a small pool is made in the sand and a fish placed in it, it stays there until the water sinks through the sand and leaves the fish dry, after which it starts to flip about apparently aimlessly. However, if a slight trickle is allowed to enter the pool, it heads up stream and tries to wriggle out of the pool if even the stream is too small to float it. In its efforts to make progress, it often makes short leaps, usually falling back in the stream again, and continues to show this simple positive rheotaxis as the only directional influence until open water is reached. In the case of a stream flowing out of a shrinking puddle a negative rheotaxis is sometimes evident. As these experiments were not carried on in an identical manner to those of Mast's, nor as extensive, the only real divergence in results appears to be in the matter of going uphill which none of the present fish did at all.

However in the related *Rivulus* directional locomotion over land is common.

Leaping.

The leaping of fishes may be considered simply as a rapid swimming up through the surface of the water, momentum alone carrying the fish forward after the tail has left the water entirely. In leaping, the passing into air, a less dense medium, comparatively accelerates the speed and makes possible leaps that otherwise would appear too great for what seems to be slight effort. The active propulsion is obtained in water, a dense medium, with its patent advantages of comparative solidity whilst the glide produced by momentum is in a light medium which has comparatively little resistance. The course the fish takes after leaving the surface is dependent on the manner in which the body is held and is modified by external forces, such as wind velocity and the angle of its direction to the fish. If the body is held rigidly in a straight line the path will be straight, barring external factors. *Mugil* usually leaps in this manner. If the body is flexed, the fish follows the curve and falls to the concave side. *Salmo* and *Tarpon* usually show this. The final stroke before leaving the water is often of great amplitude in these fishes and sends them upward in a great curving path.

Flying.

Much of a controversial nature has been written concerning the flight of fishes, that is, as to whether they fly in the strict sense or simply soar, and as Clark (1925) suggests there is probably some truth in both views, That is, probably it is largely a soaring flight, although there is a strong probability that distinct wing movements of muscular origin aid them at times, especially in the case of the very young in which the wings vibrate through a relatively large arc with a distinct "hum." However, the pectoral muscles of the exocoetids are approximately equal to those of the hemiramphids (Ridewood, 1913). At least some of the vibration of the pectorals of large examples is due to the forcing of them, as planes edgewise through the air, and some according to J. T. Nichols, is likely a muscular quiver incident to holding the "wings" out under tension. Ridewood regards the flying characins, *Gastropelecus*, as more likely true flyers on anatomical grounds, although the observed behavior of *Thoracocharax* would hardly lead to this conclusion (see page 250 and Fig. 73, A). The wings of the exocoetids are ideally suited for soaring, as indeed is the entire fish, from an aeronautical point of view, as Dowd (1921) points out. Other flying fishes, *Pantodon* and the Dactylopteridae, are less well equipped and their flights are of shorter duration and comparatively clumsy.

Allied to this type of flight is the skimming or skittering over the surface, of hemiramphids, etc. Here the pectorals are only sufficient to raise the weight of the head and forepart of the body into the air, leaving the tail submerged. The bulk of the fish being in the air, reduces head resistance considerably, while the tail still has the advantages of operating in the denser medium. Flying fishes pass through this stage as a transitory one as they leave the water at the beginning of a flight and lapse back into it if their momentum ceases and they do not wish to entirely submerge again.

The latter they generally accomplish by a short leap and a head first plunge. When the tail is so submerged it is violently oscillated. This naturally vibrates the entire animal. Being supported in such a precarious manner this is especially noticeable at the tips of the "wings" on account of their position. This may have been contributary to the belief that the wings are actually flapped in locomotor effort. Such aerial excursions start as a simple leap.

Comparison, Interrelation and Discussion.

The chief locomotor efforts of fishes other than swimming are represented as specializations, none of which is the common property of a large number of fishes. Further, these various specializations are more or less mutually exclusive. That is to say that burrowing fishes do not fly and leaping forms do not creep as a rule. On account of the narrow limitations of most of these specializations and their, for the most part, evident operation they are only touched on here, the lesser details being discussed in their proper places in "Part II—Systematic."

REOMORPHISM.[8]

For the most efficient rapid motion through water a torpedo-like form is essential, varying somewhat in detail with the actual speed. That is, it should be circular in cross section throughout and somewhat cigar shaped. Of course, this ideal is never attained in fishes as there must always be some apparatus for applying the driving force and changing the course when necessary as well as other structures not at all concerned with mobility, such as the defensive and offensive requirements call for. The closest approach to the ideal is seen in oceanic pelagic forms not concerned directly with either surface or bottom, for in animals living close to a plane of division and under the positive or negative influence of gravity a marked dorso-ventral differentiation is present. Du Bois-Reymond (1914) believes a sharply pointed anterior end on a fish to be desirable for high speed but points out that it is physiologically impossible, all of which is clearly untrue. He was apparently unfamiliar with the modern studies of streamline forms and the experiments proving that a comparatively blunt nose is the ideal and did not realize the existence of such spear-like forms as *Tylosurus* and *Lepisosteus*, not to mention a host of less exaggerated types.

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[8] First used by Karrer (1924). Defined as designating "the structural adjustment in organism toward streamline contours."

It seems likely, judging from the existing diversity of fish heads, that any desirable entering section could be evolved, and probably those existing on high speed fishes are nearly theoretically correct. See Parsons (1888) for a discussion of the forms of fishes from a mathematical standpoint. The maximum speed that various fishes can attain is largely undetermined, but is considerable in some, especially oceanic forms. Stringham (1924) gives the following estimates in miles per hour for some freshwater species: Salmon, 6.75 to 7.0; Pike, 8.0 to 10.0; Alewife, 6.8. None of these approach the speed of some pelagic forms.

The normal speed of a fish, its maximum velocity, the length of time it can maintain it, its locomotor classification, its normal bathometric habitat, its agility, maneuvering, leaping ability, et cetera, are all reflected in every external structure. Even to the most untrained eye such reflections serve as a fairly accurate gauge of the mobility of an example. With some study and experimentation, a really accurate measure of the method of movement may be visualized and even an average illustration will reveal unmistakable indications of locomotor ability.

The shape of the body is no doubt truly streamline for the normal speed at which a given fish is built to move, modified according to the mechanical necessities of locomotor efforts or other requirements (Houssay, 1911, 12 and 14), except where motion is normally so slow that the pressure differential due to movement is entirely inconsequential. Here streamline shape is usually sacrificed for armature or some adaptation not directly concerned with locomotion. Some torpedo-like form is absolutely necessary if any relatively high speed is to be attained. Reference to "Part II—Systematic" will reveal instances where, what are apparently anything but streamline shapes, in reality are excellent ones, considering the other necessary factors, and are simply disguised by the peculiar locomotor apparatus of the possessor, *e. g.* some of the Batoidei. The investment of the body, usually imbricated scales, forms another reflection of the locomotor prowess of the possessor. Primitively they are metameral, being grouped in the same number of vertical rows as are the myomeres. Specialization has changed this in various ways, in some cases removing them completely, as in the Siluridae, where a tough flexible skin replaces them, and increasing them in others as in the Pleuronectidae, where

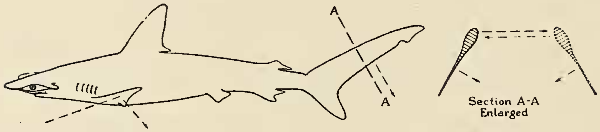

Fig. 63. Diagram of an epibatic tail as in *Sphyrna*. The diagonal dashed arrows indicate the manner of impingement of the caudal and pectorals in horizontal swimming. The section A–A indicates the swinging of the dependent part of the caudal.

there are less myomeres than rows of scales. That is, the scales are placed according to the lines of strain incident to the body flexures (Ryder, 1892). Primarily they were designed as a flexible armor and still generally retain that function although in some cases, such as the Ostraciidae, flexibility has been completely sacrificed for armature strength (See also Woodward, 1893). The mucous covering of the body in most cases doubtless reduces skin friction considerably, not only because of its inherent slipperiness, but also because it fills up any small irregularities, such as spaces between the teeth of ctenoid scales, and makes the fish actually smoother than it feels to the hand, because the pressure of the latter passes through the mucus so readily. The position, shape, prominence and sculpturing of the scales all reflect the natatorial nature of the possessor. This is likewise true of outstanding armor of any kind, which is always sacrificed by fast swimming fishes, the slower ones only being able to afford it.

The fins as well as the body form, especially the caudal fin, form a very fine index of speed and agility, the same types being repeated over and over again in the most unrelated fishes of similar habits of swimming, being in many cases beautiful illustrations of homodynamic adaptations.

Various types of tails are generally considered by taxonomists, such as heterocercal, homocercal, dyphycercal, isocercal and protocercal. The fact that homocercal tails are heterocercal internally need not concern us here, for it is the fin as a whole that presses against the water, and its exterior which measures its reaction and not the details of the internal osteology. We may better use the terms epibatic for externally heterocercal tails; isobatic for tails externally symmetrical, no matter what may be the internal structure, and hypobatic for tails with an enlarged and thickened lower edge as in *Exocoetus*. Whether all tail fins are strictly homologous or in some cases merely analogous need not concern us here either.

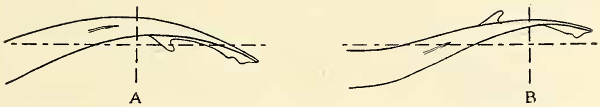

Fig. 64. Diagram of the action of a bilobed epibatic tail as in *Mustelus*. A, position of upper and lower lobe to one side of body when they are both on the same side of the crest of one wave. B, position of upper and lower lobe on alternate sides of the body when they are on either side of the crest of the same wave a little later.

The primitive epibatic tail (heterocercal) is unsymmetrical about a horizontal plane passing through the axis of the body in that the vertebrae margin it above. As the rest of the tail depends from this it follows that being flexible, the tail would wave from side to side in its passage from right to left (Fig. 63). The pressure would be alternately downward from side to side as indicated in the enlarged section A–A. This would tend to raise the tail and pitch the nose downward, were it not for the pectorals being held out at an appropriate angle. Indeed, the fins of sharks are almost permanently fixed at this angle. Daniel (1922) has shown by pinning the pectorals down that fish with epibatic tails under such conditions always head downward and are then unable to rise. Fig. 64 shows such an epibatic tail from above in two successive positions. In A both the upper and lower lobe is pressed to one side, that is, when they are both on the same side of the crest of one wave. When this has travelled back as in B to where it splits between them, the lower lobe switches to the other side and is later followed by the upper so that they are again on one, but the opposite, side of a crest. While the crest is between them it is clear that the two lines of pressure are diagonally opposed, thus forcing the tail forward in a line more nearly parallel and closer to the axis of progression. This is obviously an economy which tends to reduce the oscillation of the nose.

In the isobatic (homocercal) tail, there is no tendency to lift or depress the tail, the force all being in a horizontal plane. The various forms this type of tail may take are discussed on pages 226 to 229 together with the special contours of the epibatic tail. Fig. 65 compares the two types. The acuminate isobatic (diphycercal) type appears only where all locomotor efforts have been removed from that organ and have been transferred, for example, to the anal, as in *Gymnotus* (Fig. 48 B).

The hypobatic tail is a comparatively rare structure associated

Fig. 65. Comparison of an isobatic and epibatic tail. A, isobatic tail as in *Pomatomus*. B, epibatic tail as in *Mustelus*.

with flying fish and their kind. The action is naturally the reverse of the epibatic and apparently has some bearing on the frequency with which they ascend rapidly in preparation to flight or skittering over the surface.

The many and various shapes of the tails of fishes are indicative of the speed and type of movement enjoyed by the different forms that use movements of the body for propulsive effect. Fishes with large squarish or spatulate tails, as *Promicrops, Micropterus* and *Ephinephalus* are comparatively slow but are capable of extremely sudden short spurts of speed, but never of long continued high speed efforts. Fishes with deeply forked or lunate tails are capable of long continued swimming at high velocity, the more lunate the tail the faster being the fish as in *Coryphaena, Pomatomus* and *Sarda.* These tails from tip to tip span a distance equal to from 18 to 25 per cent. of the total length, and frequently the accompanying narrow peduncle is strengthened with keels. Twelve high speed fish averaged 21 per cent. in this proportion. Extremely slow speed fishes, in which the tail functions as a propellor very slightly, are unforked and proportionally large, as in *Alutera.*

Heterocercal tails while generally forked, at least in the Salachii, subscribe to the same generalization as is evidenced by the fast *Isurus* of open waters with its crescentic tail and by the sluggish *Ginglymostoma* of littoral environs in which the tail is very slightly notched and asymmetrical. Again in inland waters, *Polyodon,* fast as compared to *Amiatus* and *Lepisosteus,* exhibit the same contrast although the large awkward rostrum of the former to some extent interferes with swift motion. In the Selachii, an evenly oval cross section is associated with a nearly symmetrical tail, while a subtriangular section is associated with an asymmetrical tail. This condition again reflects a bottom and pelagic habit. Certain fishes with forked caudals show a very slight prolongation of one lobe over the other as in *Rachycentron* in which the upper lobe is slightly larger, and in many characins the lower is somewhat produced. It hardly seems possible that these slight differences could have locomotor significance, or at least in the present state of our knowledge to attribute such would be mere speculation.

Nichols (1915 and 20) gave the substance of the following as an explanation of the fork in fishes' tails. As the bodies of speedy fishes are streamline forms, the water that is displaced forward moves around the fish from front to rear more rapidly than does the fishes' motion relative to the water outside the limit of its influence. For a maximum efficiency this displaced water should meet immediately on leaving the converging curves of the body. A square tail would prevent this and thereby offer some impedance as it causes a parallel run of the water after, in the interests of economy, the two streams should have merged. Also, by placing the functional tips of the caudal fin well above and below this point of confluence, a much better purchase is had on the water, which at these points is not moving away from the fish so rapidly. While this hypothesis is believed to be true, there are other probably equally important factors. Furthermore, Nichol's idea does not give a positive reason as to why some tails are squarish, it being left as an assumption that a fish moves more rapidly if its tail happens to be forked. If an ordinarily spatulate tailed individual has a prominent fork cut in the tail, no greater speed is attained nor is it visibly reduced, but the motion of the body is different for reasons explained on pages 228 and 229. On the other hand, if a "comet" goldfish (*Carassius auritus*) with its cumbersome and over-developed tail, produced by artificial selection, has it so trimmed as to be similar to that of a common or "plain-tailed" goldfish, it will attain the normal locomotion of the species,[9] although these often seem to be considered as fishes of speed. An explanation of what the changes in the body movement accompanying a trimming of the tail indicates is superfluous, because the following description of the ostraciiform model treated in a similar manner serves better in its stead.

Both a forked tail and a square tail, otherwise similar, were constructed for the model (see Appendix) so as to be interchangeable.

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[9] In performing this experiment care must be exercised in the selection of an example. One should be taken with a normal body, as frequently a change in shape in the body accompanies this excessive size of the tail. A young example is preferable, for generally old fish, even if normally bodied at first, are so modified by being forced to manipulate this excessive growth for a long time as to be worthless in this experiment.

The difference in the model's action was studied comparatively, from which the following was found:

With a square tail. The highest speed attained with this tail, less than the following, was obtained by adjusting it to move through an arc of about 35°. A larger swing of the tail with such a large surface caused so great a swing of the nose that the motion lost in that manner impeded forward progress to a considerable extent.

With a forked tail. The highest speed attained with this type of tail, higher than the above, was obtained by movement through an arc of about 70°. The amplitude of the swing of the nose was not increased as rapidly as it was in the case of the former with the increased caudal amplitude, for there was less resistance to the passage of this tail of lessened area (about one-fourth less) through the water. This, on the other hand, formed a less effective blade on account of the reduced surface of pressure. It is evident that a forked tail swinging through a wide arc is more suited to fast movement than a square one of larger area, and also more efficient than a square tail given less amplitude. In these experiments the driving mechanism was set to move at a definite speed with no load applied. As various loads were then placed on the clockwork motor, it slowed down proportionally. As the greater the resistance offered to the tail the slower its movement became, the speed of progression stood as an index of the thrust of the various tail forms. The connecting mechanism was so designed as to give one complete cycle of the tail's oscillation for each revolution of the driving shaft. As this was true for any amplitude, it follows by the laws of leverage, that the short strokes were more powerful than the longer ones, it taking the same force to produce each. From this, it is inferred that for a continuous high speed a deeply forked tail oscillating through a large arc is more easily manipulated than a large one making short strokes and eating up more energy on account of the accompanying great swing from side to side of the nose, which is lost motion.

The fact that water particles impinging on the tail fin near its base attain a more nearly backward path may have something to do with shaping the tail in fast swimming forms (Fig. 43). That is, the center part of the tail is cut away reducing the amount of area that gives more of a sidewise and less of a directly backward thrust, with its accompanying large deflection of the head. Coupled with Nichol's factor, this effect is probably of considerable importance.

Other experiments with the model concerning caudal fins demonstrated the following: the more flexible the tail, the less the nose oscillates. This would naturally follow for a flexible tail gives a more nearly backward thrust than a rigid one, as explained on pages 171 to 173. If such a flexible tail be made long enough, a complete sine curve or more will be formed *i. e.*, the anguilliform type carried on by momentum. This calls to mind the motion of tadpoles and spermatozoa. As fish tails are all more or less flexible,

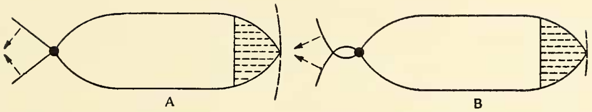

Fig. 66. Comparison of action of model with a rigid and a flexible tail. A, with rigid tail. B, with flexible tail. The dashed arrows indicate the angles of pressure. The dashed curves at the nose indicate the amount of its swing.

it follows that the really extreme ostraciiform type as seen with such a rigid tail as in the model is never actually encountered in life. Fig. 66 compares the motion of a rigid and flexible tail on the model and the accompanying oscillation of the nose.

As a further demonstration of the differential pressure of such a tail movement due to its position at the end of the body, the following is given.

> If the tail is not secured perfectly rigid to the turning support and accurately centered, it will eventually work itself around to one side causing the model to take an inward spiral path. (Fig. 67) first three positions. After this has gone on for a time and the tail oscillates equally about a line drawn at right angles to the axis of the boat through the tail post, it simply turns on a point as in the fourth position (Fig. 67). After the tail passes this position and the major part of each oscillation is anterior to this line, the model starts to back up and spirals outward until halted by the tail slapping against the side of the hull, as in the final positions (Fig. 67). This forcing of the rudder around on its not too tightly secured axle can only be accounted for by the presence of less resistance to the second half of a stroke than to the first. That is, the part of the stroke which causes the nose to deflect most sharply is less in resistance than the part which chiefly moves the boat ahead. In the moving boat the passage of it through the water with the consequent currents flowing aft must have nothing to do with it for if they controlled such a loosely fastened tail, their effect would be to keep it centered and even if started off center they would return it. It seems to be referable to the oscillation of the anterior part. This would indicate that after once being started the nose swings largely by momentum on the last half of a stroke with speed nearly as great as that of the caudal causing little pressure to be felt from the flowing water relative to the tail fin. In backing out of the spiral the tail acts like one pectoral fin as described under Pectoral Propulsion.

Pectorals of a spatulate form accompany fishes of slow or moderate speed, while long falcate, or at least not spatulate ones, accompany rapid swimmers which use them largely for wheeling and seldom if ever for either propulsoin or backing water.

The actual form of the ventrals appears to be of little significance in rapid swimming, they being for the most part auxiliary maneuvering instruments or at best "bilge keels." They are uniformly kept tucked close to the body in rapid swimming. Generally

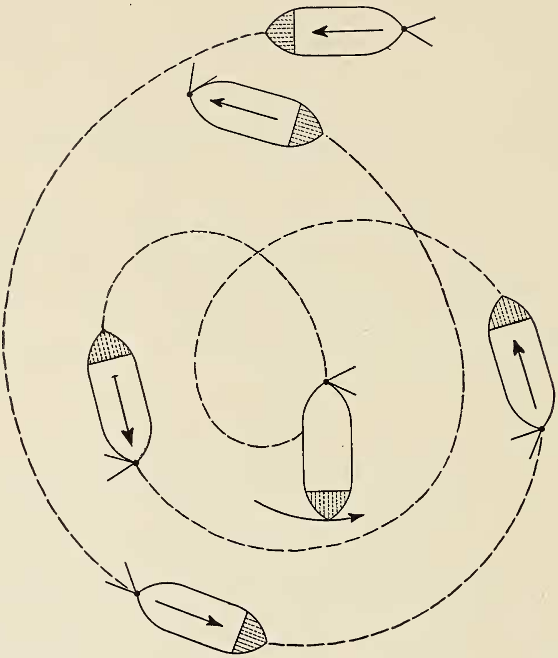

Fig. 67. Behavior of model with tail fin insecurely attached to shaft. The arrows indicate direction of travel. Note that the tail oscillates progressively more and more to one side.

considered, they are the fins that fishes can best dispense with, excepting the dorsal or anal in certain forms. They are the only fins on which the primary locomotor significance is not placed in some forms. Examples are numerous of cases of the predominant importance of all other fins, *e. g.* caudal, *Micropterus;* pectoral, *Raja;* dorsal, *Gymnarchus;* anal, *Gymnotus.* Also they are the fins most frequently modified to such an extent as to lose all locomotor function, as seen in *Phycis* and *Colisa,* and not infrequently they are entirely missing. These facts coupled with the experiments described on pages 215 and 216, lead to the belief that the pelvic fins are of comparatively minor locomotor importance. Their form generally follows that of the pectorals quite closely. See also "Starting and stopping."

The dorsal and anal fins in fast fishes are generally somewhat similar in size and shape and it is only in relatively slow forms that any great developments of one over the other is seen. However, there seems to be a general tendency for the anal to be somewhat shorter than the dorsal. The reasons for this appear to be two fold. The anal cannot very well extend forward of the vent with economy for several anatomical reasons, which by reference to the preceding parts should be clear, as well as probably for phylogenetic reasons. The pelvics appear to compensate for lack of length of the anal, acting as "bilge keels" as pointed out above, for, primarily, the dorsal and anal are keels. Comparatively elongate forms that have the pelvics greatly reduced or wanting, generally have the anal unusually long with the vent often displaced forward. In the fastest forms the vertical fins can be depressed so completely as to mar the perfection of the streamline form in no way at all. In fishes with their greatest bulk above a line from the tip of the snout to the middle of the peduncle, the dorsal is generally larger than the anal and conversely, when the bulk is below that line, the anal is generally larger; whereas in fishes nearly symmetrical about such a line, these fins are practically equal in size as noted by Abel 1925. This appears to be merely a placing of these steadying keels at the point of greatest vantage. A fish if inclined to roll will do so about this line, giving the greater bulk the largest swing on which a steadying keel would be most effective.

The remaining parts not mentioned specifically including axillary scales. produced fin rays, erectile processes, either employed for locomotor or other purposes or both, are formed according to streamline necessity in proportion to the speed desirable to the possessor. As these are specializations usually of a limited character they are treated under their respective heads in Part II—Systematic.

The chief external characters of fishes affected by or affecting locomotion may be tabulated according to their variations. Such a table follows, its purpose being to make more clear the broad gamut of variations through which fishes range, although it should be borne in mind that there is no attempt to go into details, simply the main elements being indicated, with their extreme modifications and the norm between them.

This table lists the principal elements of fishes' external topography and gives their chief ordinary range of variation. It is believed that the list is complete in a broad way, *i. e.*, that any species could have its various elements checked off according to the eleven items, which with their various descriptive divisions

TABLE III

Elements	*Variation*
Center of gravity	Vertical position (High—Median—Low)
	Horizontal position (Anterior—Median—Posterior)
Shape of body	Longitudinal Elongate—Fusiform—Truncate)
	Transverse (Depressed—Cylindrical—Compressed)
	Special (Bizarre—Rotated through 90°—etc.)
Surface of body	Protective Covering (Naked—Scaled—Rugose and armored)
Snout	Relative Length (Attenuate—Medium—Blunt)
Mouth	Size (Large—Medium—Small)
	Position (Superior—Terminal—Inferior)
Gill opening	Size (Large—Medium—Small)
	Shape (Slit-like—Oval—Circular)
	Vertical position (Superior—Median—Inferior)
	Special (Multiple—United below—etc.)
Dorsal and Anal	Length (Long—Medium—Absent)
	Height (High —Medium—Absent)
	Shape (Lobate—Rectangular—Falcate)
	Special (Multiple—Produced rays—etc.)
Caudal	Length (Long—Medium—Absent)
	Spread (Great—Medium—Absent)
	Shape (Spatulate—Truncate—Forked)
	Type (Epibatic—Isobatic—Hypobatic)
	Special (Prehensile—Produced rays—etc.)
Pectorals and Ventrals	Length (Long—Medium—Absent)
	Height (High—Medium—Absent)
	Shape (Spatulate—Medium—Falcate)
	Vertical position (High—Medium—Low)
	Horizontal position (Anterior—Medium—Posterior)
	Special (Sensory rays—Intromittent organs—etc.)

could be placed in one category or another. It would be found if a large number of species were tabulated according to this list that they would fall into certain rather constant groups. That is, certain characters are definitely associated with others. For example, fish with spatulate pectorals do not have forked tails, fishes with falcate pectorals are never exceedingly elongate, and so on. This brings us to what is probably the most important consideration, one not shown by the tabulation itself. That is the relationship of these factors, as above noted and not their absolute intrinsic quantities alone, determines the locomotor characteristics of a given species. It explains how fishes of different appearance may have nearly similar locomotor functions, equal speed and so on, for not alone does the absolute response determine these conditions, as the co-relation of the involved elements must be of a given sort to produce a specific result.

Relationship to habits and Development.

Habits and development are both determined by locomotor requirements and determine locomotor abilities. A few examples may be considered here.

The habit that many smaller fishes have of following larger ones, ships or almost any moving body of considerable size, may among other advantages, enable them to slip along with less effort than they would otherwise have to make. For example, a small shark following a large vessel is swimming in a flowing stream of water running toward the stern of the boat to fill up the cavitation created in moving forward. As this is running in the desired direction, the effect is the same as though the fish were being carried along by a tide. In modern screw propelled vessels the wake trends clearly forward. A small fish following a larger one receives a similar pull, but to a lesser degree because the jets, as pointed out under the section on Jet Propulsion, tend to make the wake trend backward. That they fail to do so completely, at the lower speeds at least, may be observed by watching suspended particles. The undulations of the body and other factors offset and overcome the tendency of the exhaled water to reverse the direction of the wake. In a similar manner it would seem probable the lagging members of a school dropping behind from fatigue or exhaustion would be unconsciously helped along by their more sturdy brothers swimming in the van.

A Berlin engineer, H. Schieferstein, working on the effects of tuned oscillating parts on reciprocating machines, noticed an increase in power output in machines that were made up of parts with a definite periodicity, (Gradenwitz 1923). This efficiency led him to suggest that flocking birds might gain a mutual advantage through the intervening air spaces. If this be proven true, it is more than likely that fishes in schools receive a similar mutual benefit on account of the fact that mechanical shock and vibrations are much better transmitted through water than air. Then too, it is a matter of simple observation to note how often several adjacent members of such a company are moving with perfect synchronism. More data on the entire subject of the oscillatory effects on power machines is essential before a thorough understanding of the subject relative to the schooling of fishes may be had. At least it is probable that an individual fish commonly vibrates its body in accordance with the proper frequency, considering the animal or its oscillating part as a vibrating element.

In the section "Maintaining a stationary position," mention was frequently made of movements of the various fins. Certain of these have been explained as counteracting the disturbing influence of respiration, but a considerable percentage of the movements that make it difficult to appreciate the real effect of respiration is not explainable on that basis. As these movements are, necessarily, most often neutralized by others in order to maintain a resting position, it is evident that they serve no equilibrating function. Here then is an apparent waste of effort on the part of the muscular system, from which no useful result is obtained. An illustration may often be seen in the Centrarchidae when a slight caudal undulation is accompanied by an increase in the backing efforts of the pectorals far above that necessary to offset the thrust of the exhalations. Another may be seen in *Amiatus* which at times will start a series of waves in the dorsal at its anterior end preparatory to moving forward, but before the inertia is overcome, some negative impulse causes the initiation of a similar series from the posterior end, effectively checking the reaction of the first; these opposing series meet at about half way between, and then die out.

The explanation of such muscular displays is referred to the nervous system, as it is conceived that the muscular activity observed is the visible effect of nervous impulses not altogether inhibited, as fishes in a tank or natural body of water are constantly receiving various stimuli of an opposing nature. For example, if some object be dropped into a tank containing fishes, they usually rush toward or away from it, depending on the amount of commotion it makes in breaking the surface, its size, etc. If the object be something inert, like a stone, the fishes soon quiet down again, often coming back to their previous positions. This is an illustration of a case where the reversal of the impulse follows some time after the original one. If however, some less violent stimulus, as, for instance, another fish too large to be suitable for food and too small to be dangerous, comes within the sensory range of an individual, the first stimulus will be to move, but, lagging behind this by only a fraction of a second, will come the details of size, and in this hypothetical case no change of position being necessary or desirable, the reversal of the fin movements will be nearly instantaneous.

Fishes dependent upon flight both for safety and for pursuit of food, show this characteristic of quick reversals or counter movements most strongly, if indeed they do not keep in almost constant motion. On the other hand, bottom forms such as the Rajidae, Pleuronectidae, Cottidae and Batrachidae, which depend primarily on coloration and shelter for safety, fail to show this passing over of impulses at all. In one sense the rapid alternation or starting and checking of movements might also be likened to the "dancing" of a boxer, in search of an opening for a thrust. In some forms, as *Umbra*, this activity is so definite that it may be considered a fixed and constantly present habit. It seems possible at least that this keeping open of the nervous paths may serve a useful purpose when it is necessary to make an immediate departure.

Vertebrate animals accelerate their rate of respiration on fright. This has usually been attributed to a primitive reflex preparatory to precipitous flight. In the case of many fishes whose practically only reaction to a fearsome object, under most circumstances, is flight, this increased respiration caused by fear acts directly in the actual effort of moving away from the disturbing influence, thus being a mechanical advantage as well as a purely physiological one.

The larval forms of fishes which are free to move about begin life with a sub-carangiform or even anguilliform movement, even if they develop into something entirely different subsequently, *e. g.*

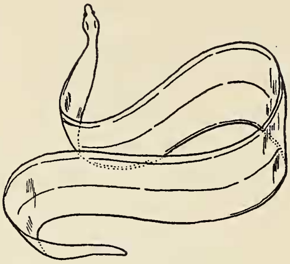

Fig. 68. Progression of a leptocephalus. *Conger* sp. After Dean (1912).

Spheroides (Welsh and Breder, 1922). This is always found to be the case, as indeed would be expected, except in very specialized incubation or developmental habits. In these cases the free swimming stage is possibly abbreviated or obliterated, and may be passed through either within the egg capsule, or in the female's body, or in some special environment; or the locomotor apparatus is functionless as a means of propulsion because of the possession of some special structure making locomotion undesirable or impossible. An example of the first case of reduction in swimming ability in the larval stage is seen in *Fundulus heteroclitus*, where the young fish do not leave the egg until they have become post-larvae with a full complement of fins, when they can swim substantially as do their parents. Any ovoviviparous fish, such as *Lebistes reticulatus*, illustrates the second case. The third is exemplified in the larvae of practically any nest building fish that stands guard over its offspring, as *Macropodus*, *Gasterosteus*, or in the larvae of any form showing oral gestation, as *Felichthys* or *Paratilapia*. The larvae of the Salmonidae are so encumbered by the great yolk sac which does not disappear until after the larval state has been well passed, that they simply lie on the bottom in passing through this stage, awaiting the yolk's absorption.

Many of the long bodied larvae, such as leptocephali, show the most extreme form of anguilliform motion to be seen anywhere (Fig. 68). The curves resemble, to a certain extent, those of a snake progressing over a very smooth surface. This movement is no doubt correlated with the extreme ribbon shape of the leptocephali, making this excessive bending relatively easy to perform. Dean (1912) mentions that he could not notice any "slip" in the progression of a larval *Conger* and that a pencil placed in one of the loops was not touched as the animal moved forward. However, Dean's Leptocephalus while apparently having a high coefficient of efficiency would have eventually touched his pencil if it had been sufficiently long. It is nevertheless remarkable that such a great amount of effective energy could be delivered. In this type of movement no orthokinetic port is formed. See page 182. As metamorphosis proceeds, this method is supplanted by the more familiar anguilliform type.

The primitive pectorals are generally spatulate in shape and early function as paddles. As they increase in prominence, the anguilliform motion decreases in those species destined to lose it, until the post-larval, and finally the adult, form of locomotion is attained.

The more special details of habit are treated under their respective heads in "Part II—Systematic."

PART II—SYSTEMATIC

INTRODUCTION.

Having considered the physical forces applied by the various types of fishes in moving about in "Part I—Physical," it now remains to examine the various major groups of living forms in order to understand how their individual specializations agree with the more general statements set forth and developed previously. In the actual work upon which this paper is based, the opposite method was naturally employed. That is, a great number of species, each usually represented by many individuals, was studied and experimented upon before the generalizations of the previous part were hazarded. It is obviously impossible for any one person to examine all extant fishes in the flesh, and it is altogether reasonable to make inferences on the belief that like locomotive structures *within one group* are applied in closely similar manners.

No attempt has been made to describe in minute detail the very small differences between closely related fishes for such variations are referable in most part to causes other than locomotor requirements. Such changes as a slightly larger or smaller number of fin rays are so bound up in the sum total of phylogeny that it is impossible to ascribe a locomotor advantage of one over the other.

If any such advantage actually exists, our knowledge of the habits of fishes is manifestly too inadequate to enable a correlation to be made that is more than grossly speculative. On the other hand, decidedly different fishes often accomplish similar results in slightly different ways because, for non-locomotor reasons, members primarily concerned with motion have secondarily acquired added and different functions, *e. g.*, the change of the anal fin in male ovoviviparous Poeciliidae to an intromittent organ.

TREATMENT BY ORDERS.

Under this section the great groups of recent fishes are considered in taxonomic order as arranged by Bridge and Boulenger in the Cambridge Natural History (1904).[10] That is, the arrangement given in that work is followed completely down to and including families. The species and genera mentioned, however, follow more recent taxonomic practice for obvious reasons. Under each grouping a very general statement is given explaining the locomotor classification or classifications into which its various members fall.[11] In many cases the general types of locomotion are so similar to others that for the present purposes a few words are sufficient and in most cases the correlation with the propelling structures is evident by referring to the previous part. To avoid repetition, page references are given to Part I, in which members of the group are discussed. Following this, specific instances and side lights on those species most closely worked with are mentioned. These are placed in smaller type as their bearing on the main theme is slight, but they serve to illustrate various points in detail and to show what sort of differences might be expected in any group not so intimately known. At the end of each group is tabulated a list of the species studied in life to enable other workers to check the present paper intelligently and to indicate the breadth of the base upon which the generalizations were based. Species in light faced type were studied by observation only, either in a state of nature, in captivity, or, in most cases, both. Those in heavy type were experimented upon in various ways as partially indicated in other parts of the paper.

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[10] This classification is used simply because of its widespread use, and its adoption here should not be taken as an endorsement of it.

[11] Acraniate forms are omitted from the present discussion as being too far removed from the chief forms under consideration to warrant inclusion for the present purposes.

CLASS—CYCLOSTOMATA

Orders—MYXINOIDES and PETROMYZONTES

These elongate jawless forms use the simple anguilliform method of necessity, as they possess no appendages of a locomotor nature. The continuous fin fold can only function if the body is used in an anguilliform manner. They are skilled at burrowing. The Petromyzontes are also able creepers, accomplishing this by aid of the suctorial mouth. See pages 203 and 219 for other data.

Petromyzon marinus, and probably all others, when swimming or forcing a passage through weeds and débris, usually folds the suctorial disc together upon itself from side to side. This makes the entrance portion of the animal regularly conic in shape, thus reducing the hindrance that would otherwise be formed by the open buccal cavity. If open, it would tend to deflect the head upwards and as these animals possess no paired fins at all, difficulty might be encountered in offsetting this deflection, as it would have to be done by exertion of the body muscles alone. Fig. 69 shows the passage of the stream lines about the head of an example both with the mouth open and closed (Breder 1923). The ability of this animal to inch its way up smooth, damp surfaces is well known and may be observed at any dam or stream frequented by them.

Species studied in life—

1. **Petromyzon marinus** Linnaeus.

2—*Lampetra wilderi* Jordan and Evermann.

CLASS—PISCES

Subclass—ELASMOBRANCHII

Order—PLAGIOSTOMI

SUBORDER—SELACHII

The typical sharks display swimming movements intermediate between the anguilliform and carangiform. *Mustelus* approaches the former and *Carcharodon* the latter. Some of the depressed forms approach the movements displayed by the Batoidei (rajiform) in certain respects. The family Rhinidae is fairly intermediate, but is closer to the skates in its movements than to the generalized sharks.

Correlated with the transition from a practically anguilliform shark to a sub-carangiform one is associated an accompanying change from an epibatic to a sub-isobatic tail and from a subtriangular cross section to a nearly elliptical one.

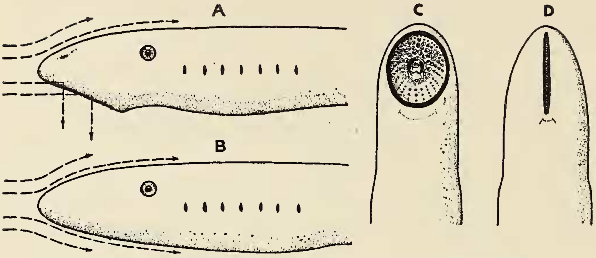

Fig. 69. Diagram illustrating the reason for *Petromyzon marinus* closing the mouth while swimming. A, head of a swimming lamprey with mouth open indicating how water below the axis of the body would be deflected downward from the mouth, thereby forcing the head up. B, head of a swimming lamprey with the mouth closed indicating how the water both below as well as that above the axis of the body would be parted without any deflecting effect. C, ventral view of the head of a lamprey with the mouth open. D, ventral view of the head of a lamprey with the mouth closed.

The function of the notch in the upper lobe of the tail is unknown, and there is a possibility that there is none today, its presence being accounted for phylogenetically, for sharks deprived of the tab certainly appear to swim as well as those with it. As the tail waves from side to side this pendant piece simply flaps from one side to the other, trailing along after the tail proper. Abel (1912) believes that the tab was originally the whole caudal fin and that a second anal migrated backward and forced the tip out to where it still remains today, while the anal became the functional caudal. This theory lacks conviction and a function may yet be ascribed to the notch. At least it is certain that this tab increases the tendency to raise the tail because of its greater flexibility.

The fins of sharks are very limited in their movements practically their whole function being that of keels and rudders. On this account, sharks are unable to make an abrupt stop, swerving to one side of an obstacle instead, for they are unable to use the pectorals or any other members as "brakes."

Many sharks, such as *Mustelus*, *Carcharhinus* and *Squalus* flex the dorsal and anal at times to aid in turning. That is, they bring the posterior parts of these fins toward the concave side of the turn. The under surface of the lobe of these fins is slightly concave and quite possibly forms a suction to the side to help hold the deflexed fins in place during the turn. See under Tarpon, page 247, for other data concerning the use of fins in this manner.

The turning over of sharks when feeding from the surface is not a necessary act, for often they will deliberately swim up, protruding the snout, so as to place the inferior mouth at the surface. However, when such turns are made, they are controlled entirely by warping the guiding keel-like fins.

See pages 194–195, 203, 226, 233, and Figs. 52, 63, 64, 65 B, for other data.

Mustelus canis when chafed by confinement will often swim up vertically through the surface of the water and hold a position with the fore part of the body exposed for some time by the continued action of the submerged hind portion. Over one-third of the body is often so lifted, and for shorter times even as much as one-half has been noted. This gives a measure of the force exerted, for it is not a matter of momentum as in leaping, but simply a direct and continued "push."

Sphyrna zygaena is believed to use the lateral expansions of the cephalic region as a bow rudder acting in a vertical plane, enabling it to rise and dive with unusual alacrity.

If *Vulpecula marina* Valmont possesses a locomotor advantage in its elongated tail, this is unknown. Allen (1923) believes that it is used as a "whip" to maim smaller fish in order to facilitate their capture.

Rhineodon typus Smith, although little known, seems to gain some advantage from its exhalations. Mr. L. L. Mowbray, in speaking of a thirty-five foot specimen taken at Long Key, Florida in June 1923, stated that in its struggles to free itself while tied by the tail, it ejected powerful jets of water through the gill slits causing a great current to flow back so strongly that a miniature breaker was formed at about the first dorsal. Also, when the fish was at rest a piece of seaweed inadvertently taken in at the mouth would be ejected violently through the gill clefts by an extra strong jet.

Species studied in life—

Family—SCYLLIIDAE

3. *Ginglymostoma cirratum* (Bonnaterre).

Family—CARCHARIIDAE

4. **Mustelus canis** (Mitchill).
5. *Carcharhinus milberti* (Müller and Henle).
6. **Carcharias taurus** Rafinesque.

Family—SPHYRNIDAE

7. **Sphyrna zygaena** (Linnaeus).

Family—SPINACIDAE

8. **Squalus acanthias** Linnaeus.

Suborder—Batoidei

The primary locomotor organs of most members of this suborder are the tremendously enlarged pectorals in which are localized

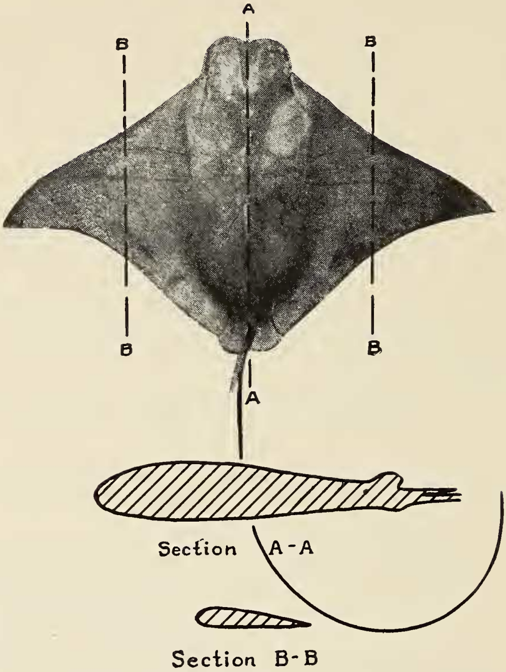

Fig. 70. Diagram of the streamline contours of *Rhinoptera bonasus*. The sections of the actual photograph A–A and B–B were made by slicing the animal shown and tracing the outlines.

anguilliform undulations in a vertical plane (rajiform Fig. 48 D). Certain examples approach the movements of the Selachii, *Pristis*, for example, being more shark-like than skate-like in its movements. These two orders intergrade completely in locomotor methods, following of necessity the changes in body form, especially regarding the degree of depression. The Pristidae have a close parallel in the Pristiophoridae among the Selachii, whereas the Rhinobatidae somewhat resemble the Rhinidae.

In the family Rajidae, the tail steers to a certain extent, being held out rigidly, although at times it may be lashed about with some trivial locomotor effect, chiefly because of the position of the reduced dorsals near its tip, which form a small but functional tail fin. The family Torpedinidae has a less expanded disc and a functional caudal fin. The pelvics have a special function when the skate is resting on the bottom; they operate to push the animal forward by kicking back much as though they were feet. Frequently in rising the members of this family give a single violent backward thrust, so launching themselves on their way. While the fish rests on the bottom, most of the excurrent water passes out through the spiracles, and on rising, if it is physically possible, the water is likely to be directed through the gill slits so as to react forcibly on the solid substratum.

The families Trygonidae and Myliobatidae have carried the rajiform undulations a step further. The tail has become a mere trailing wisp, which, while it may have some slight course-determining action, appears to trail passively after the animal. Steering is accomplished for the most part by differential action of the pectorals. That is, in curving, the outside "wing" is speeded up or the inside one retarded which swings the animal accordingly. These forms, being broader than long, do not appear superficially, to be especially well fitted for cleaving the water, although they are notably faster than the skates. One evident adaptation is the frequent loss of all rugosities which generally ornament the skates. It is clear that this apparently unhandy shape is necessary for a high development of this type of locomotion. On close examination, however, it will be seen that for a body of their peculiar shape a maximum streamline form has been developed. The longitudinal sections (Fig. 70) indicate the nature of the wedge shape of the body.

See pages 187, 207, 223, 230, and Fig. 48D, for further data.

Pristis microdon in ordinary swimming swings along with the gait of the shorter bodied sharks, such as *Carcharias*, although in addition, the edges of the large pectorals flutter. Most of this fluttering is probably incident to their motion through the water although some of it is doubtless muscular and of locomotor function. At times when frightened they will flatten themselves against the sand in a manner similar to *Raja*. Then and when very slow motion is made, the movements of the pectorals are prominent. They appear to reverse these ripples as a gentle braking action. The armed rostrum weaves back and forth somewhat as would a bowsprit on the ostraciiform model.

Raja eglanteria sometimes adheres to smooth vertical surfaces. At such times most of the exhaled water escapes through the spiracles, which may serve as a slight reactive function to hold the skate against the surface. That all does not so escape is demonstrated by the slight ripples at the posterior part of the disc caused by the water flowing from the gill slits. As they invariably head up, this must tend somewhat to offset the effect of gravity. As the fish slightly arches its body, it would seem that some suctorial effect was attempted although this would be destroyed at each exhalation allowing water to pass through the gill clefts.

Species studied in life—

Family—PRISTIDAE

9. **Pristis microdon** Latham.

Family—RAJIDAE

10. *Raja erinacea* Mitchill.
11. *Raja diaphanes* Mitchill.
12. **Raja eglanteria** Bosc.
13. *Raja stabuliforis* Garman.

Family—TRYGONIDAE

14. *Urolophus jamaicensis* (Cuvier).
15. *Dasybatus centrura* (Mitchill).
16. *Dasybatus say* (Le Sueur).
17. *Pteroplatea micrura* (Bloch and Schneider).

Family—MYLIOBATIDAE

18. **Rhinoptera bonasus** (Mitchill).

Order—HOLOCEPHALI

Nothing can serve better here than a paraphrased summary of Dean's (1906) excellent description of the behavior of *Chimaera colliei* Bennett.

As the caudal is reduced to a diphycercal wisp the force derived from metameral undulations is dependent upon the expanse of the long low dorsal and anal which are produced to the posterior extremity of the body. The large delicate pectorals appear to have two types of movement which may be used together or separately They may be used somewhat after the manner in which *Abudefduf* wings its way through the water as described under "Pectoral locomotion," or they may be undulated when held out at right angles to the body in a rajiform manner. When moving slowly these fish rock from side to side slowly showing an imperfect stabilizing effect of the fins acting as keels. Normally they are rather sluggish but at times of great excitement may show sudden spurts of speed. They sometimes rise considerably above the bottom and then sink slowly, probably after the manner of the triglids.

Callorhynchus with its decidedly epibatic tail probably approaches the sharks more in its manner of locomotion, that is, the tail is relatively more important as a locomotor organ, while *Harriota* with relatively large pectorals and an attenuate caudal appears to have the emphasis placed on the former, and doubtless some, such as *Chimaera*, have anguilliform flexures localized in the dorsal fin.

Subclass TELEOSTOMI

Order—CROSSOPTERYGII

Evidently most of these fishes swim in a manner approaching the anguilliform, although they present a certain stiffness, somewhat as in *Tylosurus* or *Esox*. Harrington (1899) writes, "Peculiar in the swimming movements of *Polypterus* is the manner in which the head moves freely from side to side. This produces the appearance of a progression more or less snake or eel-like, although in general the powerful sweeps of the strong tail characterize the progression as fish-like." Its lobate pectorals are, no doubt, used for progressional purposes at times. *Calamoichthys* is probably more similar to *Anguilla* in its mode of locomotion and little aid can be expected from the small pectorals.

The purpose of the interrupted dorsal is not clear although it may serve in a capacity somewhat similar to that of the finlets of the Scombridae. However, neither the general build of the fishes nor the anterior position of the "finlets" would suggest that such a device would be of any particular service.

Order—CHONDROSTEI

The fishes of this group swim in a manner intermediate between that of the anguilliform and carangiform type. The epibatic tail makes the warping of the pectorals imperative as with the Selachii. Likewise abrupt stops are not possible on account of the lack of an efficient "brake." The small vertical and pelvic fins allow of a considerable rolling motion which their small area does not overcome.

See page 179 for other data.

Species studied in life—

Family—ACIPENSERIDAE

19. **Acipenser sturio** Linnaeus.
20. *Acipenser rubicundus* Le Sueur.
21. *Acipenser brevirostrum* Le Sueur.
22. *Scaphirhynchus platorynchus* (Rafinesque).

Order—HOLOSTEI

The locomotor movements of this order are sub-carangiform. That is, their movements embody hardly more than one-half a sine curve, for, although they are elongate the rigidity of their bodies prevents anguilliform curves from being formed. This is no doubt associated with their heavy armature.

See pages 186–189, 202, 207, 222, 226, 234, and Fig. 48 A, for other data.

Amiatus, in addition, in much of its movement employs localized undulations situated in the long dorsal (amiiform) (Fig. 48A). The pectorals are employed largely in backing water for which their size and shape are beautifully adapted.

Lepisosteus osseus and others of the genus, on account of their long and relatively rigid bodies turn awkwardly, employing both the pectorals and pelvics in a manner which Dr. W. K. Gregory aptly likened to that of a "hook and ladder truck," there being a steering device at either end. Their stopping is made in a manner similar to that described on page 69 and illustrated by *Esox*, Fig. 57, A and B.

Species studied in life—

Family—AMIIDAE

23. **Amiatus calva** (Linnaeus).

Family—LEPIDOSTEIDAE

24. **Lepisosteus osseus** (Linnaeus).
25. *Lepisosteus platostomus* Rafinesque.
26. *Lepisosteus tristoechus* (Bloch and Schneider).

Order—TELEOSTEI

Suborder—MALACOPTERYGII

Fishes of this sub-order while showing a great range of locomotor variation generally approach the carangiform type of locomotion closely and consequently are generally strong and active swimmers. The pectoral fins, while capable of being folded back do not have the flexibility to be seen in many of the higher teleosts and are not often capable of being used effectively to back water with. Their use is more nearly like that of the sharks' pectorals, except that they are tucked away in active swimming as the tails are isobatic and consequently there is no tendency to depress the fish that requires offsetting. Their prime function is wheeling and turning. While capable of some braking action, short stops are not the rule with these fishes. A turn to avoid an obstacle is the more usual method (Clupeidae). The tails vary from truncate to forked, which is somewhat associated with a fluvitile and marine habitat respectively, although in the more specialized forms it may disappear entirely as an active fin (*Gymnarchus*). If the adipose fin, common

Fig. 71. The ultimate dorsal ray of *Tarpon atlanticus*. A, cross section. B, the tip showing the groove below.

in this group, has a locomotor significance it is unknown. As this is true of the adipose fin in other groups as well, no further mention will be made of it. Some of the members of this suborder are capable of tremendous leaps (*Tarpon* and *Salmo*), and leaping amounts to almost a group characteristic. The numerous specialized fishes in this suborder that do not conform to the above general statements include the highly specialized Mormyridae with their elongate snouts, and the Pantodontidae with their powers of flight. *Gymnarchus* (Dahlgren 1914) and *Notopterus* (Schlesinger 1910), other specialized offshoots, propel themselves by localized undulations of the long dorsal and anal respectively. The Stomiatidae with their obvious adaptations to a very special environment, and others might be mentioned, but the above will serve here for the purpose of illustration.

See pages 201, 216, 221, 223, 230, and Fig. 59A, for other data.

Tarpon atlanticus possesses a long wisp at the posterior margin of the dorsal. This is concave below and tapers to a slim point (Fig. 71). Mr. L. L. Mowbray ascribes a special and definite function to this with reference to the famed leaping habits of the species. Preparatory to making a leap, according to Mowbray, the tarpon lashes this whip around to one side of the body and clamps it tight to its side. Here it adheres because of suction as the grooved piece lifts slightly from the body at its center. The dorsal is thus held rigidly to one side, so aiding in determining the course. Even in a dead fish the adhesion is considerable when the ray is applied in the manner described. The turn is made toward the side to which the ray is adhering.

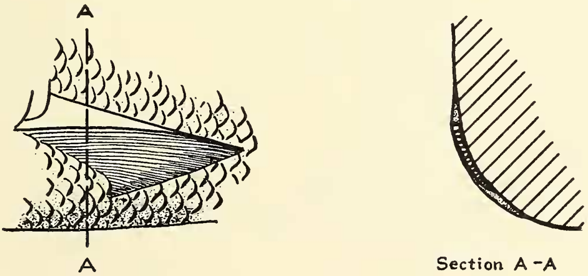

Fig. 72. The axillary scale of *Elops saurus*. Side view with fin pressed to body and section with fin in same position.

Elops saurus shows a very delicate adjustment to streamline contours in the axillary scale of the pectoral. When that fin is held flat to the body, the scale rises and occupies the triangular area immediately above it (Fig. 72), thus giving a very smooth section to this region. When the fin is extended as in wheeling, the scale drops down behind it forming a sort of chute for the water to pass over behind the fin. This is of a very gently curving form, no doubt affording a minimum of frictional resistance.

Ophisthonema oglinum possesses a similar ultimate produced dorsal ray to that of *Tarpon.* It would seem that this would serve a similar function, for even in very small examples a perceptible suction could be detected.

Thymallus ontariensis appears not to use the large dorsal at all for propulsive purposes, although its size might suggest it even if its shape and proportions do not.

Species studied in life—

Family—ELOPIDAE

27. *Tarpon atlanticus* (Cuvier and Valenciennes).
28. **Elops saurus** Linnaeus.

Family—ALBULIDAE

29. *Albula vulpes* (Linnaeus).

Family—CLUPEIDAE

30. *Clupea harengus* Linnaeus.
31. *Pomolobus mediocris* (Mitchill).
32. *Pomolobus pseudoharengus* (Wilson).
33. *Pomolobus aestivalis* (Mitchill).
34. *Alosa sapidissima* (Wilson).
35. **Opisthonema oglinum** (Le Sueur).
36. **Brevoortia tyrannus** (Latrobe).
37. *Ilisha fürthii* (Steindachner).
38. *Anchovia elongata* Meek and Hildebrand.
39. *Anchovia brownii* (Gmelin).
40. *Anchovia mitchilli* (Cuvier and Valenciennes).

Family—SALMONIDAE

41. *Coregonus clupeiformis* (Mitchill).
42. *Oncorhynchus tschawytscha* (Walbaum).
43. *Salmo fario* Linnaeus.
44. *Salmo mykiss* Walbaum.
45. **Salmo irideus** Gibbons.
46. *Salvelinus fontinalis* (Mitchill).
47. *Cristivomer namaycush* (Walbaum).
48. *Thymallus ontariensis* Cuvier and Valenciennes.

Suborder—OSTARIOPHYSI

This order divides itself into two very differently appearing groups, the Eventognathi and the Nematognathi. The former includes fishes that in the main agree closely with the general locomotor habits of the suborder Malacopterygii. There is, however, a general increase in the flexibility and use of the pectoral fins. Many cases of parallelism exist in the two groups. For example, certain characins bear more than a passing resemblance to *Salmo,* and a functional similarity exists between *Gymnotus* and *Gymnarchus,* and so on. So many of the South American Characinidae and oriental Cyprinidae are narrowly and peculiarly specialized that no one broad statement can take them all in. Generally their locomotor habits resemble more closely some type in another group, entirely unrelated, which they happen to resemble, rather than some close relative. Thus *Ctenolucius* behaves more like *Esox* than its immediate relatives. Leaping is a fairly well developed characteristic of many forms, especially those resembling the generalized Malacopterygii in locomotor habit. *Misgurnus* shows nearly anguilliform movements and in many ways approaches the Nematognathi in locomotor habits. Their relatively large pectorals are

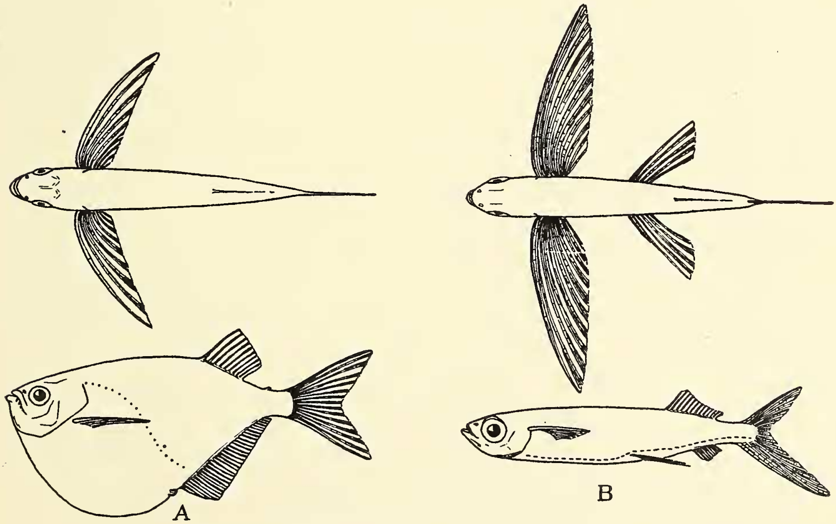

Fig. 73. Pectorals modified for flight. Dorsal and lateral views. A, *Thoracocharax.* B, *Cypselurus.*

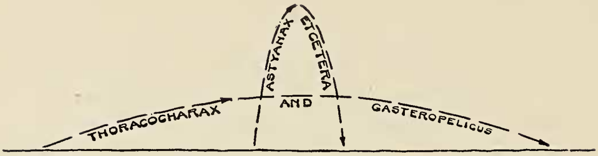

Fig. 74. The trajectory of characins. *Astyanax*, and other short-pectoraled forms. *Thoracocharax* and *Gasteropelecus*, long-pectoraled forms.

largely in the nature of planes controlling the angle of elevation.

The Nematognathi propel themselves by methods reaching from the nearly anguilliform to the carangiform and even beyond. The pectorals are largely planes as in *Misgurnus*. They are typically sluggish bottom fishes and the form of the body movements is directly correlated with their length and with the extent of their dermal armature. Thus some of the elongate naked Siluridae approach the anguilliform movements and the short, tightly incased plecostomids reach beyond the carangiform and extend toward the ostraciiform type. Some are adept at burrowing; others at creeping and still others at navigating over land.

See pages 183–185, 187–189, 196, 207, 216, 219, 221, 223, 227, 230, 236, and Figs. 48B, 53, 56, for other data.

Thoracocharax maculatus, owing to its long falcate pectorals is capable of soaring for considerable distances. Compared with the exocoetids there seems at first glance little similarity, but if viewed dorsally there is a pronounced one (Fig. 73). The similarity is even greater between these characins and the "two-winged" flying fish, *Halocypselurus*. This is destroyed in the lateral view by the greatly dilated ventral region devoted to pectoral musculature. Except for housing this musculature it probably has little to do directly with their flight. This flight seems to be the simple trajectory of a characin leap flattened by the presence of these pectorals (Fig. 74), although at times they seem to be able to sustain themselves for some little distance, and there may be some fin movement as Ridewood (1913) suggests for *Gastropelecus*.

Carassius auratus developed into monsters by artificial selection hardly need any elaboration as most of the excess finnage is clearly an encumbrance to activity which is plainly evident on inspection. Further details are given on page 99.

Synodontis membranaceus Geoffroy and some others of this genus are perfectly accommodated to swimming in an inverted position. This suggests an adjustment to a displacement of the normal center of gravity. The perfect accommodation to this habit is indicated by the complete reversal of the color differential, these species being dark ventrally (the upper half) and light dorsally (the lower half).

Astroblepus longifilis inhabiting mountain torrents is able to hold tightly

Fig. 75. The motion of *Atroblepus longifilis* overland. The portions of the caudal swing during which the mouth alternately releases and adheres is indicated.

fast to smooth surfaces by use of its suctorial mouth, both under water and out of it. The method of progressing overland as seen by the author is essentially a fish-like flapping coupled with an appropriate action of the mouth, it holding fast on the flexure of the caudal portion, and releasing on the extension (Fig. 75). The depressed body and the extended pectorals and pelvics cause it to rest easily on its ventral surface. The inching along by means of the muscles attached to the pelvic girdle as given in Evermann and Kendall (1905) for an allied species was not observed, although no doubt the rough pelvic spines with their backwardly directed spinules act as a resistance to a possible backward drag. See also Johnson (1912).

Loricaria altipinnis and other elongate loricariates with greatly depressed peduncles seem to approach the anguilliform type of locomotion, but as the peduncle is constructed to cleave the water and not react to it, virtually all of the effective thrust is centered in the caudal fin. As this then swings from side to side its action more closely approaches that of the ostraciiform type. That is, if the tail of the model be extended by an equally non-resisting rod, the effect would be nearly similar.

Species studied in life—

Family—CHARACINIDAE

49. **Curimatus magdalenae** Steindachner.
50. *Characidium marshi* Breder.
51. **Piabucina festae** Boulenger.
52. *Compsura gorgonae* (Evermann and Goldsborough).
53. *Pseudocheirodon affinis* Meek and Hildebrand.
54. *Brycon striatulus* (Kner).
55. *Aphyocharax rubropinnis* Pappenheim.
56. *Hyphessobrycon bifasciatus* Ellis.

57. **Astyanax ruberrimus** Eigenmann.
58. *Creagrutus affinis* Steindachner.
59. *Bryconamericus emperador* (Eigenmann and Ogle).
60. *Hemibrycon dariensis* Meek and Hildebrand.
61. *Gephyrocharax atricaudata* Meek and Hildebrand.
62. **Thoracocharax maculatus** (Steindachner).
63. *Roeboides occidentalis* Meek and Hildebrand.
64. **Ctenolucius beani** (Fowler).
65. *Hoplias malabaricus* (Bloch).

Family—GYMNOTIDAE

66. **Gymnotus carapo** Linnaeus.
67. *Sternopygus dariensis* Meek and Hildebrand.
68. **Hypopomus brevirostris** (Steindachner).

Family—CYPRINIDAE

69. *Carpiodes velifer* (Rafinesque).
70. *Catostomus commersonii* (Lacépède).
71. *Catostomus nigricans* Le Sueur.
72. *Erimyzon sucetta oblongus* (Mitchill).
73. *Moxostoma macrolepidotum* (Le Sueur).
74. **Cyprinus carpio** Linnaeus.
75. **Carassius auratus** (Linnaeus).
76. *Tinca tinca* Linnaeus.
77. **Scardineus erythrophthalmus** (Linnaeus).
78. *Campostoma anomalum* (Rafinesque).
79. *Chrosomus erythrogaster* Rafinesque.
80. *Semotilus bullaris* (Rafinesque).
81. **Abramis crysoleucas** (Mitchill).
82. *Notropis procne* (Cope).
83. *Notropis cornutus* (Mitchill).
84. *Rhinichthys atronasus* (Mitchill).
85. *Exoglossum maxillingua* (Le Sueur).
86. *Brachydanio rerio* (Hamilton, Buchanan).
87. *Brachydanio albolineatus* (Blyth).
88. *Danio malabaricus* (Jerdon).
89. *Puntius semifasciolatus* Günther.
90. *Puntius conchonius* (Hamilton, Buchanan).
91. *Misgurnus fossilis fossilis* (Linnaeus).

Family—SILURIDAE

92. *Felichthys felis* (Linnaeus).
93. *Ictalurus punctatus* (Rafinesque).
94. *Ictalurus furcatus* (Le Sueur).
95. *Ameiurus natalis* (Le Sueur).
96. **Ameiurus nebulosus** (Le Sueur).
97. *Schilbeodes gyrinus* (Mitchill).
98. *Clarias anguillaris* (Linnaeus).

99. **Rhamdia wagneri** (Günther).
100. **Pimelodella chagresi** (Steindachner).
101. **Pimelodus clarias punctatus** (Meek and Hildebrand).
102. *Ageneiosus caucanus* Steindachner.
103. **Astroblepus longifilis** (Steindachner).
104. *Corydoras paleatus* Steindachner.
105. **Hoplosternum punctatum** Meek and Hildebrand.

Family—LORICARIIDAE

106. *Plecostomus plecostomus panamensis* Eigenmann.
107. *Lasiancistrus planiceps* (Meek and Hildebrand).
108. *Chaetostomus fischeri* Steindachner.
109. *Ancistrus spinosus* Meek and Hildebrand.
110. **Loricaria altipinnis** Breder.
111. *Loricaria variegata* Steindachner.
112. *Sturisoma panamense* (Eigenmann and Eigenmann).
113. *Stirisoma citurense* (Meek and Hildebrand).

Suborder—SYNBRANCHII

The swimming of this group is typically anguilliform as it must be on account of the shape and lack of locomotor appendages. Burrowing is a prominent characteristic and the speed with which these fish can enter loose soil is remarkable. Their speed through open water is also comparatively great as they habitually simply dash from cover to cover never remaining in an exposed position for long.

Species studied in life—

Family—SYNBRANCHIDAE

114. **Synbranchus marmoratus** Bloch.

Suborder—APODES

These forms all show the typical anguilliform movements; those with pectoral fins using them simply in very small adjustments of position, chiefly when resting on the bottom. Their use is especially prominent when backing the cephalic part while the rest is in contact with some surface. Water expelled through the nearly circular gill openings is, of course, of use only as straight reaction, as well as on account of the shape of the body. Their very positive thigmotaxis causes the ejection of water to be of no consequence when resting. In some forms such as *Myrichthys*, in addition to the more common general body movement, undulation may be localized in the dorsal and anal.

It is interesting to note that many of these start life as ribbon-shaped larvae, the leptocephali (Fig. 68), which are pelagic in habit. As soon as the ribbon shape disappears and they become more nearly circular in cross section the pelagic habit is lost and life is taken up along shores, much of which time is spent in contact with solids.

See pages 166–169, 175–183, 219, 114, 235, 237, and Figs. 39, 45, 46, 49, 68, for other data.

Anguilla rostrata not infrequently arches its body and "coasts" downward by gravity alone, controlling the direction by turning the head and the radius of the arc which the body describes.

Species studied in life—

Family—ANGUILLIDAE

115. **Anguilla rostrata** (Le Sueur).
116. *Myrichthys oculatus* (Kaup).

Family—MURAENIDAE

117. *Gymnothorax funebris* Ranzani.
118. **Gymnothorax moringa** (Cuvier).
119. *Echidna catenata* (Bloch).

Suborder—HAPLOMI

The propulsive methods of this group are about equally divided between body movements which are sub-carangiform and pectoral efforts, although the group includes a great variety of forms. Here, for the first time, species are found in which the pectorals take a considerable part in the production of a forward thrust (barring, of course, the rajiform movements). In the long bodied forms, with the pelvics placed well behind the pectorals, the movements are somewhat as in *Lepisosteus.* In comparatively many of the short bodied forms, the pectorals take on a large share of the progressional effort. As would be expected, the more compressed forms display a greater bending of the body than do the forms more nearly circular in cross section.

See pages 202, 203, 205, 207, 210, 211, 214–215, 220, 222, 235, and Figs. 57A, B, 57, 59B, 61, for other data.

Umbra pygmaea habitually uses the pectorals to a great extent as pointed out on page 235. Their characteristic position of rest is diagonal to the surface, with the caudal portion drooping. At such times the pectorals and dorsal may show only as a blur as they move with great rapidity. What effect there may be from exhaled water is apparently taken care of by an excess of the pectoral over the dorsal action. The cycles of the pectorals and dorsal are synchronized and are about twice as fast as those of respiration. Any sudden sound causes a pronounced increase in the rate of these with no change in position. Slow forward motion is effected by the pectorals, but rapid movement by a sub-carangiform body movement.

Mollienesia latipinna at times slightly undulates the large dorsal fin (the male only) for progressional purposes.

Xiphophorus helleri in its "love play" performs its backing movements by means of the pectorals in such alteration that a hesitant movement results. Other ovoviviparous species, such as *Lebistes reticulatus*, perform in a manner closely similar in their amorous maneuvers.

Platypoecilia maculatus, being short-bodied, has a practically carangiform movement.

Rivulus uropthalmus and *chucunaque*, being longer bodied, tend to approach the anguilliform method when not employing the pectorals alone for propulsive purposes.

Species studied in life—

Family—ESOCIDAE

120. *Esox americanus* (Gmelin).
121. **Esox reticulatus** (Le Sueur).
122. *Esox lucius* Linnaeus.
123. *Esox masquinongy* Mitchill.
124. **Umbra pygmaea** (De Kay).

Family—CYPRINODONTIDAE

125. *Gambusia affinis* (Baird and Girard).
126. *Priapichthys tridentiger cana* (Meek and Hildebrand).
127. *Priapichthys darienensis* (Meek and Hildebrand).
128. *Lebistes reticulatus* (Peters).
129. *Heterandria formosa* (Girard).
130. *Phalloceros caudomaculatus* (Hensel).
131. *Mollienesia latipinna* Le Sueur.
132. *Mollienesia sphenops* (Cuvier and Valenciennes).
133. *Mollienesia caucana* (Steindachner).
134. *Xiphophorus helleri* Heckel.
135. *Platypoecilus maculatus pulcher* Boulenger.
136. *Platypoecilus maculatus ruber* Stausch.
137. *Cyprinodon variegatus* Lacépède.
138. *Jordanella floridae* Goode and Bean.
139. **Fundulus majalis** (Walbaum).
140. **Fundulus heteroclitus macrolepidotus** (Walbaum).
141. *Fundulus diaphanus* (Le Sueur).
142. *Fundulus luciae* (Baird).
143. *Fundulus bermudae* Günther.
144. *Fundulus chrysotus* Holbrook.
145. *Panchax panchax* (Hamilton, Buchanan).

146. *Panchax lineatus* Cuvier and Valenciennes.
147. *Panchax chaperi* (Sauvage).
148. *Aphyosemion australe* (Rachow).
149. *Rivulus uropthalmus* Günther.
150. *Rivulus chucunaque chucunaque* Breder.
151. *Rivulus chucunaque sucubti* Breder.

Suborder—HETEROMI

Apparently these fishes propel themselves by anguilliform or near anguilliform methods, as well as by using the long anal fin after the manner employed by *Gymnotus*. The pectorals in some forms doubtless have some locomotor function.

Suborder—CATOSTEOMI

The locomotor efforts of the majority of fishes comprising this sub-order are confined to movements of the fins. In many, the encasing armament precludes any extensive body movement. Extreme and unusual specializations of various sorts are characteristic of the group allowing of no very general statement concerning their locomotor habits beyond the above, for they range from such large pelagic forms as *Lampris luna* (Gmelin) to tiny gasterosteids and syngnathids living in very special littoral environments.

See pages 177, 194, for other data.

Apeltes quadracus and other gasterosteids have pectoral movements not dissimilar to those of *Umbra*. See page 235.

Aeoliscus strigatus (Günther) and other members of this group swim with the axis practically vertical for most part although they may assume any other position. See Willey (1902) for an illustration of this species in action.

Fistularia tabacaria Linnaeus appears not to have any locomotor function connected with the great prolongation of the central caudal ray.

Syngnathus fuscus when highly excited may lash its body into anguilliform curves but makes slight progress, the pectorals and dorsal being the chief locomotor organs. The latter is undulated as in *Amiatus*.

Hippocampus hudsonius which usually moves with the backbone in a nearly vertical position is necessarily modified accordingly. In rising or falling in the water appropriate localized undulations in the dorsal give the desired motion on account of its position. A violent flapping from side to side, coupled with the action of the pectorals drives the fish slowly forward, ventral side foremost. However, when high speed, for a seahorse, is desired it leans forward with the vertebral column nearly horizontal and undulates the dorsal in localized anguilliform fashion. The much reduced anal may also be vibrated. With these various combinations of fins, any nicety of spatial adjustment may be attained. Generally speaking, the pectorals and dorsal are used in conjunction for the fastest movements, and the higher the speed attained the nearer the vertebral axis approaches the horizontal, thus drawing the divergent forces closer together and more nearly parallel to the axis of motion, so allowing for the efficiency necessary for a given speed. See Ryder (1881) for further discussion of the locomotion of *Hippocampus*.

Species studied in life—

Family—GASTROSTEIDAE

152. *Pygosteus pungitius* (Linnaeus).
153. *Gasterosteus bispinosus* Walbaum.
154. **Apeltes quadracus** (Mitchill).

Family—SYNGNATHIDAE

155. **Syngnathus fuscus** Storer.
156. *Syngnathus mackayi* (Swain and Meek).
157. *Syngnathus elcapitanense* (Meek and Hildebrand).
158. **Hippocampus hudsonius** De Kay.

Suborder—PERCESOCES

The locomotion of the members of this group is typically sub-carangiform, except in the short deep forms where pectoral propulsion is well developed, as in the Stromatidae. In most elongate forms there is not as close an approach to the anguilliform type of motion as might be expected judging from the form alone. These, such as the tylosurids, are rather rigid fishes and exhibit no great flexibility, somewhat resembling *Esox* in simple locomotor or maneuvering efforts.

Many limited specializations are found in this group, skittering over the surface and flying, finding its greatest development here. Other members are skilled leapers.

See pages 203, 221, 222, for other data.

Tylosurus marinus in maintaining a stationary position frequently fans its tail from side to side and compensates with the pectorals. In shifting its position when so resting, which is frequently done, a single flexure of the long body accomplishes this. The forward glide so initiated is nullified by the action of the pectorals, practically turning the fish on a point. This genus and its relatives, more especially the hemiramphids, are expert at leaping and skittering over the surface of the sea. Their bodies are held at an angular elevation from the surface of about 30° or even more in an extremely rigid manner and their submerged tail is vibrated rapidly. This is usually alternated with short leaps from which they alight tail first for further activity, or may sometimes plunge head first for submersion (Fig. 76).

Cypselurus sp. and related "four-winged" forms doubtless have better control of their flight than the "two-winged" species, *Halocypselurus*, for the reason that the pelvics, which serve as posterior warping planes, give them more

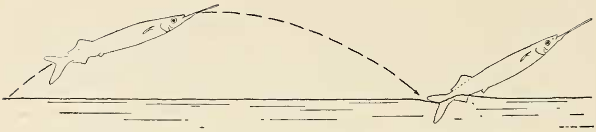

Fig. 76. *Hemiramphus* leaping and skittering. Note the functioning of the hypobatic tail in skittering.

purchase for their limited amount of maneuvering. The latter more closely resemble the flying characins, *Gasteroplecus*, etc. See Fig. 73, pages 221 and 250.

Menidia menidia, despite its somewhat elongate appearance, is an extremely stiff form. The pectorals are rather stiffly articulated and do little more than aid in turning and wheeling. They are capable of extremely sudden and rapid darts which are entirely dependent on the operation of the lateral muscles.

Mugil curema displays somewhat more flexibility than do the Atherinidae although the movements are of the same order. This genus is marked by unusual leaping ability. A straight path is followed in the leap in all cases observed by the author.

Sphyraena barracuda and related forms partake of pike-like movements except that they are inclined to show greater flexibility, in continuous swimming.

Poronotus triacanthus and related forms, such as *Peprilus paru*, are illustrative of the suppression of ventrals in short deep bodied forms. On the other hand, *Nomeus* has extremely large ones, the exact use of which is not clear. They swim both by carangiform movement and pectoral operation. However, on removal of the pectorals, they seem to be able to navigate quite well and remain in an upright position.

Channa fasciata, with its long dorsal fin has not been observed to operate it after the manner of *Amiatus*, although structurally it might well be expected to. The locomotor efforts are mainly concerned with the body muscles, which tend toward the anguilliform type. The pectorals are used as active paddles and in backing, in the conventional manner.

Anabas testudineus, being a short bodied fish living in weedy places, naturally uses the paired fins in moving about to considerable extent, and in obtaining a nicety of position. Its famed scansorial powers are apparently exaggerated or are inhibited except under very favorable circumstances. Captives removed from an aquarium appear extremely distressed, and while the operculi are thrown outward and the spines prominent, no attempt has been seen to use them except when the fish was placed in a sloping groove. Then, by the simple wriggling and flapping of the tail, the opercular spines acted rachet-like, and inched the fish slowly along.

Species studied in life—

Family—SCOMBRESOCIDAE

159. **Tylosurus marinus** (Walbaum).
160. *Tylosurus timucu* (Walbaum).
161. *Hemiramphus* sp.
162. *Cypselurus* sp.

Family—AMMODYTIDAE

163. *Ammodytes americanus* De Kay.

Family—ANTHERINIDAE

164. *Hepsetia stipes* (Müller and Troschel).
165. *Thyrina chagresi* (Meek and Hildebrand).
166. **Menidia menidia notata** (Mitchill).

Family—MUGILIDAE

167. **Mugil curema** Cuvier and Valenciennes.
168. *Mugil cephalus* Linnaeus.
169. *Agonostomus monticola* (Bancroft).

Family—POLYNEMIDAE

170. *Polydactylus octonemus* (Girard).

Family—SPHYRAENIDAE

171. *Sphyraena barracuda* (Walbaum).
172. **Sphyraena borealis** De Kay.

Family—STROMATEIDAE

173. **Peprilus paru** (Linnaeus).
174. **Poronotus triacanthus** (Peck).

Family—OPHIOCEPHALIDAE

175. *Channa fasciata* Steindachner.

Family—ANABANTIDAE

176. **Anabas testudineus** (Bloch).

Suborder—ANACANTHINI

This group is marked by a tendency toward elongation and in contrast to the preceding by a considerable flexibility. Thus the movements are typically of a type approaching the anguilliform, the comparative slenderness of form being an index of the approach to this type of movement. The Macruridae, possessing an attenuate caudal however, doubtless make use of their long anal by the application of localized undulations, and possibly also the pectorals to a considerable extent.

See page 230 for other data.

Microgadus tomcod often uses the pectorals to wing its way along in a somewhat labriform manner.

Phycis regius has been observed to bury itself in sand and reclining on its side with the head protruding, watch the movements of other fishes with apparent interest.

Phycis chuss in turning sometimes has its low long dorsal and anal flexed far to the outside of the curve. This is just the opposite of that which would cause the turn. Therefore it is inferred that the controlling muscles are simply relaxed and the water pressure causes this outward bend, it being only seen to occur in comparatively slow motion, and when other turning efforts were being obviously applied.

Species studied in life—

Family—GADIDAE

177. *Merluccius bilinearis* (Mitchill).
178. **Microgadus tomcod** (Walbaum).
179. *Gadus callarias* Linnaeus.
180. *Lota maculosa* (Le Sueur).
181. *Phycis regius* (Walbaum).
182. *Phycis tenuis* (Mitchill).
183. *Phycis chuss* (Walbaum).

Suborder—ACANTHOPTERYGII

DIVISION—PERCIFORMES

This great division while showing numerous specializations is marked by a carangiform or sub-carangiform type of body movement. As the body is short generally, frequently more so than that of *Caranx,* this necessarily follows, and even in some a faint suggestion of the ostraciiform movement is present. This group contains fishes of the greatest body depth known. Pectoral locomotion is common and used to a large extent in certain families, such as the Labridae and Scaridae, and a few forms, such as *Malacanthus,* make use of dorsal and anal undulations.

See pages 175, 189, 194, 197, 207, 208, 215, 216, 226, 230, 236, and Figs. 50, 58, 59C and D, 60, 65A for other data.

Aphredoderus sayanus with its large fins is sluggish and almost clumsy in its use of them in moving slowly about amid the weedy places it inhabits.

Pomoxis annularis and the other generalized centrarchids are covered in the preceding section and need no especial treatment here.

Thulia arge reminds one more of a characin in general swimming than its closer relatives.

Boleosoma nigrum and the other darters use the pectorals in making their characteristic darts, usually a single stroke of them being all that is made before coming to rest again.

Malacanthus plumeri, an unusually elongate form for this group, according to Mowbray uses both the anal and dorsal for locomotor purposes by means of localized undulations.

Menticirrhus saxatilus, *Eques acuminatus* and others of these two genera make considerable use of a pectoral type of propulsion, although it is not otherwise especially characteristic of the Sciaenidae.

Species studied in life—

Family—BERYCIDAE

184. **Aphreoderus sayanus** (Gilliams).
185. *Holocentrus ascensionis* (Osbeck).

Family—CENTRARCHIDAE

186. *Pomoxis annularis* Rafinesque.
187. *Pomoxis sparoides* (Lacépède).
188. **Ambloplites rupestris** (Rafinesque).
189. *Chaenobryttus gulosus* (Cuvier and Valenciennes).
190. **Enneacanthus obesus** (Baird).
191. *Mesogonistius chaetodon* (Baird).
192. *Lepomis auritus* (Linnaeus).
193. **Lepomis pallidus** (Mitchill).
194. **Eupomotis gibbosus** (Linnaeus).
195. *Micropterus dolomieu* Lacépède.
196. *Micropterus salmoides* (Lacépède).
197. *Kuhlia arge* Jordan and Bollman.

Family—CYPHOSIDAE

198. *Kyphosus sectatrix* (Linnaeus).

Family—LOBOTIDAE

199. *Lobotes surinamensis* (Bloch).

Family—NANDIDAE

200. *Badis badis* Hamilton, Buchanan.
201. *Polycentrus schombergki* Müller and Troschel.

Family—PERCIDAE

202. *Stizostedion vitreum* (Mitchill).
203. *Stizostedion canadense* (Smith).
204. **Perca flavescens** (Mitchill).
205. **Boleosoma nigrum olmstedi** (Storer).
206. *Etheostoma flabellare* Rafinesque.

Family—SERRANIDAE

207. *Roccus lineatus* (Bloch).
208. *Roccus chrysops* Rafinesque.
209. *Morone americana* (Gmelin).
210. *Cephalopholis fulvus* (Linnaeus).
211. *Epinephelus adscensionis* (Osbeck).
212. *Epinephelus striatus* (Bloch).

213. *Epinephelus guttatus* (Linnaeus).
214. *Epinephelus morio* (Cuvier and Valenciennes).
215. *Hypoplectrus puella* (Cuvier and Valenciennes)
216. *Promicrops itaiara* (Lichtenstein).
217. *Mycteroperca venenosa* (Linnaeus).
218. *Mycteroperca bonaci* (Poey).
219. *Myctoperca olfax* (Jenyns).
220. *Mycteroperca phenax* Jordan and Swain.
221. **Centropristes striatus** (Linnaeus).
222. *Diplectrum formosum* (Linnaeus).
223. *Pseudopriacanthus altus* (Gill).
224. *Neomaenis griseus* (Linnaeus).
225. *Neomaenis jocu* (Bloch and Schneider).
226. *Neomaenis apodus* (Walbaum).
227. *Neomaenis aya* (Bloch).
228. *Neomaenis analis* (Cuvier and Valenciennes).
229. *Neomaenis buccanella* (Cuvier and Valenciennes).
230. *Neomaenis synagris* (Linnaeus).
231. *Ocyurus chrysurus* (Bloch).
232. *Theropon jarbua* (Froskål).
233. *Centropomis unionensis* Bocourt.
234. **Pomatomus saltatrix** (Linnaeus).

Family—SCIAENIDAE

235. *Cynoscion regalis* (Bloch and Schneider).
236. *Bairdiella chrysura* (Lacépède).
237. *Sciaenops ocellatus* (Linnaeus).
238. *Leiostomus xanthurus* Lacépède.
239. *Micropogon undulatus* (Linnaeus).
240. *Menticirrhus americanus* (Linnaeus).
241. *Menticirrhus saxatilis* (Bloch and Schneider).
242. *Aplodinotus grunniens* Rafinesque.
243. *Pogonias cromis* (Linnaeus).
244. *Eques acuminatus* (Bloch and Schneider).

Family—GERRIDAE

245. *Eucinostomus californiensis* (Gill).

Family—PRISTIPOMATIDAE

246. *Haemulon parra* (Desmarest).
247. *Haemulon sciurus* (Shaw).
248. *Haemulon plumeri* (Lacépède).
249. *Haemulon flavolineatum* (Desmarest).
250. *Brachygenys chrysargyneus* (Günther).
251. *Bathystoma striatum* (Linnaeus).
252. *Bathystoma rimator* (Jordan and Swain).
253. *Anisotremus surinamensis* (Bloch).

254. **Anisotremus viriginicus** (Linnaeus).
255. *Orthopristis chrysopterus* (Linnaeus).

Family—SPARIDAE

256. *Stenotomus chrysops* (Linnaeus).
257. *Calamus bajonado* (Bloch and Schneider).
258. *Calamus arctifrons* Goode and Bean.
259. **Lagodon rhomboides** (Linnaeus).
260. *Archosargus unimaculatus* (Bloch).
261. *Archosargus probatocephalus* (Walbaum).

Family—MULLIDAE

262. *Upeneus maculatus* (Bloch).

Family—CHAETODONTIDAE

263. *Chaetodipterus faber* (Broussonet).
264. *Chaetodon ocellatus* Bloch.
265. *Scatophagus argus* (Bloch)
266. **Pomacanthus arcuatus** (Linnaeus).
267. *Pomacanthus paru* (Bloch).
268. *Angelichthys isabelita* Jordan and Rutter.
269. **Angelichthys ciliaris** (Linnaeus).
270. *Angelichthys townsendi* Nichols and Mowbray.

Family—TEUTHIDIDAE

271. *Teuthis caeruleus* (Bloch and Schneider).
272. *Teuthis hepatus* Linnaeus.
273. *Teuthis bahianus* (Castlenau).

Family—OSPHROMENIDAE

274. *Macropodus cupanus cupanus* (Cuvier and Valenciennes).
275. *Macropodus cupanus dayi* Kohler.
276. *Macropodus chinensis* (Bloch).
277. *Macropodus opercularis* (Linnaeus).
278. *Betta splendens* Regan.
279. *Colisa fusciata* (Bloch and Schneider).
280. *Colisa lalia* (Hamilton, Buchanan).

Family—CICHLIDAE

281. *Haplochromis multicolor* Hilgendorf.
282. *Hemichromis bimaculatus* Gill.
283. *Cichlasoma nigrofasciatum* (Günther).
284. *Cichlasoma faceatum* (Jenyns).
285. *Cichlasoma calobrense* Meek and Hildebrand.
286. **Cichlasoma umbriferum** Meek and Hildebrand.
287. *Cichlasoma tuyrense* Meek and Hildebrand.

288. *Cichlasoma maculicauda* Regan.
289. *Aequidens coeruleopunctatus* (Kner and Steindachner).
290. *Neetroplus panamensis* Meek and Hildebrand.
291. *Geophagus crassilabris* Steindachner.
292. *Pterophyllum sclare* (Cuvier and Valenciennes).

Family—POMOCENTRIDAE

293. *Eupomocentrus leucostictus* (Müller and Troschel).
294. *Abudefduf saxatilis* (Linnaeus).

Family—LABRIDAE

295. *Lachnolaimus maximus* (Walbaum).
296. *Harpe rufa* (Linnaeus).
297. **Tautoga onitis** (Linnaeus).
298. *Tautogolabrus adspersus* (Walbaum).
299. *Iridio radiatus* (Linnaeus).
300. *Iridio bivittatus* (Bloch).
301. *Thalassoma bifasciatus* (Bloch).
302. *Doratonotus decoris* Evermann and Marsh.

Family—SCARIDAE

303. *Pseudoscarus quacamaia* (Cuvier).
304. *Pseudoscarus plumbaeus* Bean.
305. *Scarus caeruleus* (Bloch).
306. *Sparisoma abligardi* (Bloch).
307. *Sparisoma viride* (Bonnaterre).
308. *Sparisoma hoplomystax* (Cope).

Division—SCOMBRIFORMES

In this group are found those forms after which the carangiform type of locomotion was named. They are a rather stiff bodied aggregation, and even the longer forms represent movements close to the above named type. The pectorals are typically stiff and without much mobility and are used almost entirely for wheeling and turning. Abrupt stops are unknown. They are mostly fast swimmers of great endurance. The relatively great amount of muscular tissue speaks eloquently of the extraordinary natatorial powers, as does the beautiful response of body and appendage form to streamline conditions. Considering these fishes as machines their relatively small "furnaces" and large propelling "engines" imply that they must consume their "fuel" rapidly, if only to be able to provide room for more, that is, they run their "boilers" at a high rate and on readily "combustible" materials of high grade. The fact that they have a high body temperature for fishes is noteworthy in this connection. This is contrasted with many sluggish fishes that live on relatively indigestible foods and work it through long digestive tracts while quietly poking around, as for example, *Catostomus*. The following percentages are based on data gathered by Corson (1923) and illustrate this proportion roughly.

TABLE IV

Species	*Percentage of viscera to entire weight*
Gymnosarda alleterata (Rafinesque)	.05 +
Thunnus thynnus (Linnaeus)	.05 —

See pages 175, 183, 194, 203, 207, 211, 216, 226, 227, and Figs. 44, 45, 47, 57C for other data.

Caranx crysos in common with the other slimmer peduncled forms, has a prominent strong keel flanking it which doubtlessly functions chiefly as a strengthening brace.

Rachycentron canadus when adult has pectorals that are shark-like in shape and use. There is, accompanying this, a slight approach to an epibatic condition of the tail, the upper margin being very slightly longer than the lower and somewhat stiffer, which may possibly be connected in some way with the manner in which the pectorals are used. In this connection it might be mentioned that the young (about 80 mm. long) have large, fan-shaped isobatic tails and use the pectorals in a labriform manner.

Sarda sarda and other forms with finlets apparently use them as multiple rudders. Their proximate margins are slightly concave and it seems that they adhere to the body as do the dorsals of *Tarpon* and some sharks. The exact mechanical advantage of these finlets is not clear although it may be that it allows an unhampered continual use of the caudal and body movements. Here again in the Scombridae, the peduncle is strengthened with a keel or keels if slender.

Istiophorus nigricans (Lacépède) must possess a powerful keel in the enlarged dorsal fin but its exact use is not evident, although it is reputed to project the fin above the surface and actually sail by that means.

Species studied in life—

Family—CARANGIDAE

309. **Seriola zonata** (Mitchill).
310. *Selar crumenopthalmus* (Bloch).
311. *Caranx hippos* (Linnaeus).
312. **Caranx crysos** (Mitchill).
313. *Caranx ruber* (Bloch).
314. *Alectis ciliaris* (Bloch).
315. **Vomer setapinnis** (Mitchill).
316. *Selene vomer* (Linnaeus).
317. *Trachinotus falcatus* (Linnaeus).

318. *Trachinotus goodei* Jordan and Evermann.
319. *Trachinotus carolinus* (Linnaeus).

Family—RHACHICENTRIDAE

320. *Rachycentron canadus* (Linnaeus).

Family—SCOMBRIDÆ

321. *Scomber scombrus* Linnaeus.
322. *Scomber colias* Gmelin.
323. *Sarda sarda* (Bloch).
324. *Scomberomorus maculatus* (Mitchill).

Division—ZEORHOMBI

This division contains greatly compressed forms with short bodies, whose locomotion must be typical for fishes of such proportions, excepting those that have developed an asymmetry concomitantly with their habit of lying on one side. These, the Pleuronectidæ, even when swimming retain the reclined position, although the undulations of the body go on as before. This places the plane of undulation in a vertical position from which fact the family name is derived. The great compression of the body makes comparatively short undulations possible, and while viewed in profile, they must be considered short and deep, their movement approaches that of the anguilliform because of the above mentioned thinness. The exhalation from the under gill slit no doubt aids in the send-off, by its impact on the bottom, as do both those of the skates. Turning is effected partly by the paired fins and partly by movements of the body.

See page 203, for other data.

Pseudopleuronectes americanus as well as others, in slow movement over the bottom undulate the marginal dorsal and anal with the tips of the rays in contact with the solid substratum thereby securing greater thrust.

Lophopsetta maculata and probably all pleuronectids in resting on the bottom often draw the anterior rays backward and the posterior ones forward so bracing themselves against any strong current that might tend to dislodge even so flat a form. In inaugurating a sally to the open water, they hasten their start by pushing off by means of the fringing rays. Fig. 77 shows this and indicates how the rays are thrust back after such a start. It is clear that the caudal portion of the fin and the first few rays have the most effect because of the larger arc through which they swing.

Achirus fasciatus attaches itself to smooth surfaces by pressing the fringing fins downward and raising the central part of the body thus producing considerable suction. In fact, most of the members of the present family possess

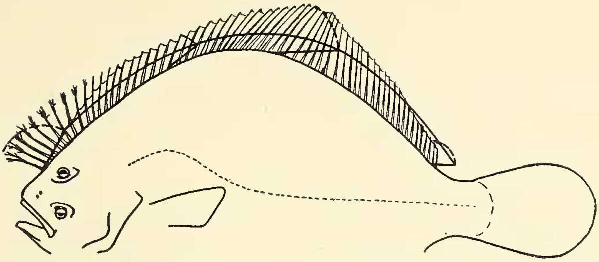

Fig. 77. *Lophopsetta maculata* with dorsal fin rays in a resting position with the manner in which they are thrown back in starting indicated. Four rays are shown in the new position with the path their tips traversed, as well as the margin of the fin. The anal operates in a similar way.

this faculty to a slight degree, but it finds its greatest expression in this genus. Vertical surfaces are even commonly so clung to.

Species studied in life—

Family—PLEURONECTIDAE

325. **Paralichthys dentatus** (Linnaeus).
326. *Paralichthys oblongus* (Mitchill).
327. *Pseudopleuronectes americanus* (Walbaum).
328. *Lophopsetta maculata* (Mitchill).
329. *Etropis microstomus* (Gill).
330. *Citharichthys gilberti* Jenkins and Evermann.
331. **Achirus fasciatus** Lacépède.
332. *Achirus panamensis* (Steindachner).

Division—KURTIFORMES

The single species of this division necessarily must confine its body movements to the carangiform, partly on account of its general shape, but more especially because of the anterior stiffening effect that the ossification of the outer membrane of the swim-bladder implies. Very likely the long anal is the seat of localized undulations and the pectorals of flapping movements somewhat like those of the Labridae.

Division—GOBIIFORMES

This group is marked by a quiescent nature. Many of the species behave in a manner quite similar to the darters, swimming from place to place simply by single strokes of the pectorals between rests. A sub-carangiform method of propulsion is found in others.

See page 219 for other data.

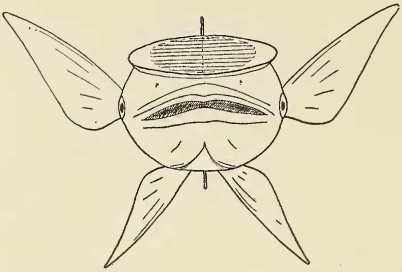

Fig. 78. Front view of *Echeneis naucrates*. Note positions of the paired fins.

Philypnus maculatus, a comparatively well rounded form; has rather small pectorals and leads a more active life than do such species that are prominently flattened above and possess large pectorals.

Sicydium salvini and other forms with united ventrals by employing them as a sucker are enabled to remain in one place in a strong flow without active muscular effort. Species studied in life—

Family—GOBIIDAE

333. *Dormitator maculatus* (Bloch).
334. *Dormitator latifrons* Richardson.
335. *Eleotris pisonis* (Gmelin).
336. *Eleotris picta* Kner and Steindachner.
337. *Philypnus maculatus* (Günther).
338. *Sicydium salvini* Grant.
339. *Gobius soparator* Cuvier and Valenciennes.
340. *Gobius daguae* Eigenmann.
341. *Microgobius miraflorensis* Gilbert and Starks.

Division—DISCOCEPHALI

The swimming movements of this group vary from a subcarangiform to an anguilliform type depending on the length of the species considered. The paired fins, of nearly equal size, are placed one pair over the other, so that when viewed end on, as in Fig. 78, they almost divide the fish into quadrants. This placing of these fins appears to be associated with the ability of the fish to rotate on its longitudinal axis in swimming, apparently turning to any such position with ease. This is clearly necessary to insure attachment to sharks or other bodies. That fishes of such natatorial powers possess such a highly specialized organ as the cephalic disc is interesting, for they have apparently suffered no particular degeneration of their power to care for themselves in a locomotor sense, for of course they must first catch their shark. In this connection, their square tail is of special significance as short spurts of speed are naturally requisite.

Echeneis naucrates, an elongate form frequently attached itself to the glass front of its tank and indulged in what appeared to be the regular swimming motions. A careful measurement (traced on tissue held against the glass) showed the tail's tip to describe an arc, the chord of which equaled 29% of the entire length of the fish. While the head was of course restricted in its movement on account of the attaching disc, the tail's tip swung an arc of just 15° or 7.5° to either side of the axis as measured from a point over the axis vertebra.

Remora remora is skilled at leaping for a fish of its build, whereas the former being much longer bodied is not.

Species studied in life—

Family—ECHENEIDIDAE

342. **Echeneis naucrates** Linnaeus.
343. *Remora remora* Linnaeus.

Division—SCLEROPAREI

The body movements of this group are sub-carangiform in the main. Being bottom fishes, the pectorals of many are developed as propelling organs which they use much as do the darters and some gobies. In others, such as the Triglidae, the pectorals are used as gliding planes and still in others, the Dactylopteridae, they are carried a step further and the fishes rise from the surface of the water by means of their large "wings," somewhat after the manner of the exocoetids, but less successfully. However, the wings vibrate rapidly and their flight has been compared to that of grasshoppers. It seems likely, however, that the vibration is a mechanical effect caused by the plane-like fins being forced edgewise through the air.

The Cyclopteridae are said to be able to creep over rocks by manipulating their ventral sucker.

See pages 203, 221, for other data.

Prionotus evolans and *carolinus* when ceasing active swimming generally extend their large pectorals and the weight of the fish (although it possesses a swim-bladder) which is heavier than the water generally, enables them to glide forward at will, wheeling about by "warping" the planes. Sometimes they will "volplane" through the water in wide circles by this means alone.

Species studied in life—

Family—COTTIDAE

344. *Uranidea gracilis* (Heckel).
345. *Cottus ictalops* (Rafinesque).
346. *Myoxocephalus octodecimspinosus* (Mitchill).
347. *Myoxocephalus aeneus* (Mitchill).

Family—TRIGLIDAE

348. *Prionotus carolinus* (Linnaeus).
349. *Prionotus evolans strigatus* (Cuvier and Valenciennes).

Division—JUGULARES

This division shows typically an intermediate position between the anguilliform and carangiform types of movement, although some approach the former closely. The ventrals may be reduced to a few rays in bottom forms or united to form a sucking disc somewhat similar to that of some of the gobies. The movements of such forms are generally quick darts made in a manner not very dissimilar to those made by the darters, some gobies and the Cottidae.

Species studied in life—

Family—BLENNIIDAE

350. *Labrisomus nuchipinnis* (Quoy and Gaimard).
351. *Blennius pholis* Linnaeus.
352. *Blennius cristatus* Linnaeus.
353. *Salariichthys textilis* (Quoy and Gaimard).

Family—BATRACHIDAE

354. *Opsanus tau* (Linnaeus).

Division—TAENIOSOMI

These deep water forms, Du Bois-Reymond (1914) states, move forward slowly by means of undulating the long dorsal. He doubts that they can effect an anguilliform movement on account of their extreme thinness and delicacy, but apparently fails to realize that at the depth at which they normally live, this delicacy disappears as in all deep water forms in their natural habitat. Schlesinger (1911, a) has shown that they undulate the body in curves of large amplitude, not unlike those of the leptocephali of apodal fishes, as well as employing the method mentioned by Du Bois-Reymond. The peculiar caudal doubtless forms an efficient rudder, and may possess a somewhat epibatic effect.

Division—ATELAXIA

The locomotion in this group is probably highly similar to that of the preceding. The body is doubtless convoluted in an anguilliform manner and similar movements are probably localized in the long low dorsal. The extremely attenuate caudal wisp is, however, probably without any particular course-determining significance.

Suborder—OPISTHOMI

The movement of *Mastacembelus* appears to be somewhat after the manner of *Gymnotus* and *Gymnarchus* combined, and not simply anguilliform as sometimes illustrated, although it is likely that they resort to such a method when high speed is requisite. That is, in general locomotion both the dorsal and anal are seats of localized undulation.

Suborder—PEDICULATI

These highly specialized fishes show a sub-carangiform movement when body contortions are attempted. The angulated paired fins are used as paddles and in many cases resemble feet more than they do fins, the mechanics of which are evident.

See page 194, for other data.

Lophius piscatorius pushes the body along the bottom at times by kicking back with the ventrals. Swimming is accomplished by undulating the caudal portion of the body, the large head having small sidewise motions.

Ogcocephalus vespertilio (Linnaeus) and other similar forms are reputed to use the fore and hind "limbs" in a manner reminiscent of frogs, the latter aiding in launching them on their way.

Species studied in life—

Family—LOPHIIDAE

355. *Lophius piscatorius* Linnaeus.

Suborder—PLECTOGNATHI

DIVISION—SCLERODERMI

This division is marked by an emphasis of the locomotor efforts being placed on the fins and a suppression of them in the trunk. In the rigidly encased forms, such as the Ostraciidae, the typical ostraciiform movement is seen, from which group it derives its name. The dorsal and anal are typically a seat of localized anguilliform undulations, especially if rather lengthy as in *Balistes* (Fig. 48C) or of localized ostraciiform movements if short as in *Lactophrys*.

See pages 166, 169–175, 177–183, 187, 194, and Figs. 40, 41, 42, 43, 48C, for other data.

Balistes vetula and others possess a long movable pelvis, which when erected seems to act as a keel. This is usually done on coming to a stop and at times when other fishes would erect their anal.

Lactophrys triqueter and others of the same genus make comparatively slight efforts to escape when held in the hand. Even the jets which may be quite powerful at times are not ordinarily forced into action. The dorsal and anal, being very short are most frequently simply waved from side to side although at times a few small waves may form at their tips. The nearly spheroidal shape of the young (10 mm.) make their movements very sluggish and irregular as would be expected.

Species studied in life—

Family—BALISTIDAE

356. **Balistes carolinensis** Gmelin.
357. *Balistes vetula* Linnaeus.
358. *Canthidermis maculatus* (Bloch).
359. *Melichthys piceus* (Poey).
360. *Monacanthus hispidus* (Linnaeus).
361. *Monacanthus ciliatus* (Mitchill).
362. **Alutera schoepfii** (Walbaum).
363. *Alutera scripta* (Osbeck).

Family—OSTRACIONTIDAE

364. **Lactophrys triqueter** (Linnaeus).
365. *Lactophrys trigonus* (Linnaeus).
366. **Lactophrys tricornis** (Linnaeus).

Division—GYMNODONTES

The extreme shortness of body of most of the members of this division limit them to an ostraciiform or sub-ostraciiform movement when the lateral myomeres are employed. However, the emphasis is placed on the pectorals, dorsal and anal in all forms known to the author. The force of the exhaled water is of considerable significance if from simple reaction alone.

See pages 187, 190, 194, 202, 236, and Figs. 51, 55, for other data.

Lagocephalus laevigatus most frequently fans its dorsal and anal from side to side (localized ostraciiform motion) in unison, but occasionally alternates them. The significance of this is not clear.

Species studied in life—

Family—TETRODONTIDAE

367. **Spheroides maculatus** (Schneider).
368. *Spheroides harperi* Nichols.
369. *Spheroides sphengerli* (Bloch).

370. *Spheroides testudineus* (Linnaeus).
371. **Lagocephalus laevigatus** (Linnaeus).

Family—DIODONTIDAE

372. **Chilomycterus schoepfii** (Walbaum).
373. **Diodon hystrix** Linnaeus.

Subclass—DIPNEUSTI

The appendages of *Lepidosiren* are nearly useless as locomotor organs on account of their size and shape but doubtless aid in maneuvering, while in *Neoceratodus* they must be of considerable importance. An intermediate between the anguilliform and carangiform types of movement is here obtained, with a close approach to the former in some cases.

LOCOMOTION OF FOSSIL FISHES.

Although our knowledge of the earlier groups is fragmentary and that of their methods of locomotion is necessarily in the nature of inferences based on anatomical similarities to living forms, the physical forces at play in moulding these ancient fish bodies were the same in early geological ages as now, so by comparison a reasonable degree of certainty as to their methods of progression may be obtained, for it has usually been the external locomotor parts which have been preserved. Probably the most interesting fact to be brought out in this connection is that fishes have not been forced or able to make any great fundamental improvement in their methods of propulsion since the earliest pre-gnathous forms swarmed in Silurian and Devonian seas. True it is that a great number of highly specialized forms have arisen, but practically all these are kinds that have not given rise to great groups, since the specializations are of such natures as to confine them to more or less restricted areas and make them utterly unfit for wide dispersion or differentiation *inter se.* Examples are seen in *Hippocampus, Histrio,* etc., but as before mentioned, fishes which are still distinctly recognizable as such, that is, are still somewhat ichthyized, all use some form of undulation, generally in the body itself, or at least localized in certain members for purposes of progression. Even the examples used as exceptions have carried these undulatory methods along with them in little altered form to their remote positions, *e. g.* the dorsal and pectorals of *Hippocampus.* It may be truly said that no known fish, living or fossil, whatever be its modification for

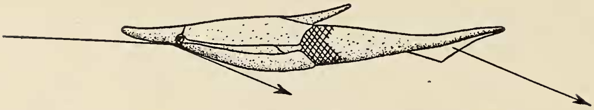

Fig. 79. *Pteraspis rostrata.* Note the manner in which the curve of the rostrum deflects the water so as to offset the action of the epibatic tail.

progression over solid surfaces, has ever been able or found it desirable to completely shake off the heritage of some form of undulatory movement for general progression while free in the water. This would seem to indicate that the optimum in method of animal locomotion through water had been reached long ago, as far as the limits of biological structures permit. It is equally true that for simple mechanical reasons, if nothing else, the effect of the exhaled water has had to be reckoned with, either as an advantage or disadvantage dependent on whether forward motion was desirable or not, from about the same early period.

Examining such early forms of pre-gnathous fish-like animals as the Ostracodermata, we find among the Heterostraci such forms as *Pteraspis rostrata,* which, if the current restorations are correct, must have progressed somewhat after the manner of modern teleosts which are nearly rigid anteriorly. The anterior region was corseletted in a calcified test, from which extended a posterior tapering portion covered with small rhomboidal scales. Of this much we are certain and it is believed that the tail was heterocercal (epibatic). Only one inference can be drawn from the fact that the animal was covered with a scaly protection posteriorly, and that is that it was to gain flexibility. The restored length almost precludes the throwing of this section into a complete sine curve. Therefore it is believed that these fish had a motion not unlike that previously described as carangiform. The caudal could not have been decidedly epibatic, or horizontal swimming would have been impossible unless the shape of the snout acted somewhat after the manner of the pectorals in the sharks of today, as suggested in Fig. 79, for as far as known, this creature lacked any other appendages except the dorsal spike, which could hardly have even any function as a keel on account of its small blade area, unless it supported a membrane. The fact that the paired fins were wanting is of small consequence, as the tadpoles of frogs, for example, manage to swim rather effectively today without them, although of course all such forms have isobatic tails, to say nothing of the surprising degree of success attained by teleosts deprived of their accustomed fins. The only loss seems to be one of a nicety of positional adjustment. It would seem that the pectorals were originally developed to offset the deflection of an epibatic or hypobatic tail, and when once well established took on other significance.

That *Pteraspis* was a free swimmer can hardly be doubted on account of its fusiform outline. Others of the same order seemingly propelled themselves similarly. *Drepanaspis* was probably a slow moving bottom form and probably could lash its tail into about one half a sine curve. Little can be said of *Thelodus* and *Lanarkia* as not much more than a crushed outline of them has been preserved.

In the Osteostraci a similar manner of locomotion was doubtless employed, but in the case of *Cephalaspis*, the test covered a short anterior portion and we know there was a metameral arrangement from there on posteriorly which no doubt corresponds to and is possibly homologus with the myomeres of the modern fishes. In this case, it may have been possible for the animal to throw itself into a full sine curve, although it is likely that it used less than this usually, probably swimming after the manner of the shorter bodied loricariates of today. The well developed dorsal "fin" formed a satisfactory keel and the pectoral lappets doubtless offset the action of the epibatic tail in driving the head downward. even though they appear to be much less flexible than pectoral fins.

Passing on to the order Anaspida, we find a great group of fusiform animals which were doubtless somewhat free swimming in habit. The metameral arrangements of the body segments and the well developed caudal fin make it almost certain that these primitive forms swam in the manner roughly similar to the modern generalized cyprinids or characins. The anal fin functioned as a keel, while the dorsal row of spines probably aided it in that function to some extent. The pectoral appendages established by Kiaer (1924) might have been predicted on account of the tail form, for, as previously pointed out, only animals with isobatic tails can dispense with them, unless there is some other substituting factor.

In the Antiarchi, we have bottom forms encased anteriorly and flexible posteriorly as the scale-like covering indicates. These forms so far as known drove themselves forward in a manner similar to the pteraspids, but with this difference,—that they had in addition well formed dorsal and pectoral appendages. Just what function these structures had is not clear, but in swimming they were probably used somewhat after the manner of pectoral fins in turning and wheeling whilst they no doubt functioned also, while the animal was on the bottom, as ambulatory organs.

In the Arthrodira, we find more conventional forms which evidently swam much after the fashion of modern fishes of similar general shape, and it is hard to imagine them lacking pectorals, on account of the tail form. The anterior armor extended nearly half way back, thus delimiting the effective undulation to the posterior part of the body which no doubt in this case means that they were limited to not more than half a sine curve. Their dentition indicates a raptorial habit and as a consequence they were necessarily powerful and comparatively fast swimmers, as their form indicates.

Among the first true jaw-bearing fishes, the Acanthodii are prominent. These forms had a full complement of fins and the gills opened externally by separate clefts as in modern sharks. They varied from short bodied fishes to those of rather elongate shape and judging from the squamation, were apparently flexible from the skull backward. The short bodied ones no doubt propelled themselves in a nearly carangiform manner while the longer forms probably threw their bodies into a greater number of curves. The single spine supporting each fin allowed of no localized undulations as the posterior margins were adnate to the body. The probability is that the paired fins were used exclusively for wheeling and turning and offsetting the epibatic depression, while the median ones were simply keels. Here, for the first time, we find the gill clefts definitely marked as such and as they are in the conventional position and appear typical, we must assume, in the absence of evidence to the contrary, that these Devonian fishes must have gained some forward thrust from the exhaled water, as has been shown for recent fishes. This, coupled with the structure of the pectorals indicates that they must have moved somewhat after the manner of sharks and were unable to make abrupt stops, turning to avoid obstacles. From here on in all groups we find similar thoracic exits for the excurrent water, and further specific mention of them is not necessary.

The Cladoselachii, while phylogenetically rather different from the above, have many points in common with them from a locomotor standpoint, but as all were elongate, they probably formed more than one wave in moving forward. The better and more highly developed caudal suggests a greater speed than the acanthodians were capable of and the cartilage rays of the fin suggest more flexibility in these members and a consequent greater use than was possessed by the former. That is, they were probably able to "warp" the pectorals in a manner which slightly approached these movements in modern sharks.

It seems reasonable to suppose that the Ichthyotomi undulated the long dorsal after the manner of *Amiatus* or *Gymnarchus*, holding the body rigid, and they may have paddled with the pectorals and pelvics as well, for these seem fitted for this method of movement. They represent the first forms with what appears to be really flexible paired appendages, such as are not again found until we come to the less primitive Teleostomi. Being swamp-inhabiting forms, it is probable that these latter two methods were employed for nice adjustments of position, as in the above mentioned *Amiatus* of today.

The fossil dipnoans so nearly resemble the recent forms in general external formation, that what has been written concerning them applies equally well to Dipterus, the most primitive of them, while fossils of higher groups (Chondrostei, et cetera) more closely resemble recent forms and need no separate treatment, being strictly comparable to recent forms. That is, the fossil sharks, actinopterygians and crossopterygians are comparable with their various recent representatives, or, by parallel development, to other groups modified only by slight or obvious changes in form and structure. Various parallelisms are apparent, for example, *Chirothrix* being apparently a flying member of the Haplomi.

PART III—CONCLUSION

RECAPITULATION AND DISCUSSION.

After analyzing the movements of fishes in the preceding two parts, we may review them from a broader aspect and consider the fundamental characteristics that are concerned with locomotion. Following is a tabulation of the larger divisions into which the swimming movements of fishes are divided, with an example showing each characteristic.

TABLE V

Type of Flexures	Location of Flexures		
	Body	Median Members[12]	Pectorals
Anguilliform	*Anguilla*	*Gymnotus*	*Chilomycterus*
Carangiform[13]	*Caranx*	*Balistes*	*Lepomis*
Ostraciiform	*Lactophrys*	*Lagocephalus*	*Scarus*

The only other swimming efforts of fishes, the exhalations of jets, may be considered in the following tabulation, using the same examples as those of Table V.

TABLE VI

Effect of Jets	Type of Gill Orifice		
	Slit	Oval	Circular
Induced Streamline	*Caranx*	....	....
Intermediate	......	*Lactophrys*	....
Simple Jet Reaction	......	....	*Chilomycterus*

These two tables (V and VI) include all the basic efforts which fishes employ in swimming and trace them through their various modifications. This at once brings out forcibly the truth of the similarity of these undulatory movements. The only one not included in Table V is the "Caudal undulation" of page 189, not of great importance to any fish. This, at times, is similar to the dorsal movements of *Hippocampus*, and with it completes the list of every known fundamental motion. It will be noted that metamerism of the activating muscles is basically present in all, only in the ostraciiform pectoral oscillation is it reduced to a practically single muscular act; in all others, at least two or more units act serially. Even in the oldest fossil forms this same condition obtains. There is thus a great uniformity underlying this superficial diversity.

Regarding Table VI little need be added, for it simply indicates that with a change from a slit-like opercular aperture to a circular one, whatever the significance of the exhaled water may be it changes from the induced streamline effect of Paxton to that of simple jet reaction. Note also that slit-like opercular ports are accompaniments of swift fishes with fusiform bodies and that other shaped exhalant vents not ejecting the water in a sheet are the property of fishes not especially fast nor of a shape directly responsive to streamline contours.

The body forms of fishes unless so modified as to be of no streamline value at all, such as *Ogcocaphalus*, vary from the elongate

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[13] "Carangiform" is used here in a comparative sense, as an intermediate between "Anguilliform" and "Ostraciiform" in reference to "Median members" and "Pectorals." See pages 189-190.

through the fusiform to the truncate. The central condition, "fish-like," is that of high speed, whilst either extreme is slower. The continuation of carangiform movements in elongate types (anguilliform) gains for the fish greater pressure areas from its sides directly, but loses the terminal effect of the tail fin. In fact, the caudal fin is generally entirely lost, as it would be practically valueless in the extreme elongated forms. Here the direct thrust of the insinuating body is the sole propellor. The truncate fishes, being unable to flex their bodies effectively on account of their shortness, have the locomotor emphasis placed on the appendages. In these fishes armature can be afforded as the body flexures cease to be important and speed is impossible. Thus other protection is desirable.

The fins, paired or median may be various but they run a similar gamut as far as their positions and forms allow. That is, they may partake of either anguilliform or ostraciiform movements. The carangiform is hardly represented in its true sense, but the intermediate type of movement may be considered as such, as indicated in Table V. The median fins if long and low have anguilliform undulations localized in them; if high and short, they have ostraciiform movements. The pectorals if wide have the former, and if narrow the latter.

The only movements which remain to be considered are those not to be considered as swimming, *i. e.*, creeping, flying, et cetera. These are all narrow specializations which have no special bearing on the present connection, as they represent in each case a divergent off-shoot of rather limited possibilities.

With this resumé, the major groups of fishes may be listed according to their chief locomotor characteristics. Table VII thus tabulates twelve factors, each with three divisions, either extreme and the norm between them. While it does not pretend to be absolute or entirely complete, the belief is entertained that it gives a true representation of these twelve characteristics in all of the groups of fishes down to Divisions. X in a column indicates the presence of the condition mentioned at its head. The placing of an X not directly in a column, but between two, indicates an intermediate condition. Dashes indicate entire absence of the condition, or, in the case of certain fossil forms, incomplete information.

It is evident in such a tabulation of intergrading factors and elements, that in many cases only an approximation can be given

TABLE VII

Classification	Body												Longitudinal Structures[14]						Pectoral									Caudal						Gill Orifice		
	Flexures			Form			Section			Flexibility			Flexures			Form			Flexures			Form			Flexibility			Type			Shape					
	Anguilliform	Carangiform	Ostraciiform	Elongate	Fusiform	Truncate	Compressed	Cylindrical	Depressed	Stiff	Intermediate	Flexible	Anguilliform	Intermediate	Ostraciiform	Long and low	Intermediate	Short and high	Anguilliform	Intermediate	Ostraciiform	Broad	Intermediate	Narrow	Stiff	Intermediate	Flexible	Epibatic	Isobatic	Hypobatic	Acuminate	Truncate	Bifurcate	Slit	Oval	Circular
Class Cyclostomata[15]																																				
Order Myxinoides	×			×				×				×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		×		×					×
Order Petromyzontes	×			×				×				×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		×		×					×
Class Pisces																																				
Sub-class Elasmobranchii[15]																																				
Order Pleuropterygii		×			×			×				×	—	—	—		×		—	—	—		×		×			×				×		×		
Order Ichthyotomi		×			×			×				×	×			×					×	×					×		×		×			×		
Order Acanthodei		×		×	×			×			×		—	—	—		×		—	—	—		×		×			×					×	×		
Order Plagiostomi																																				
Sub-order Selachii	×	×		×	×		×	×	×		×	×	—	—	—		×		—	—	—		×		×			×					×	×		
Sub-order Batoidei		×			×	×		×	×		×	×	×				×		—	—	—	—	—	—	—	—	—	×			×	×	×	×		
Order Holocephali	×	×		×	×		×					×				×			×	×	×	×					×	×	×		×		×	×		
Sub-class Teleostomi																																				
Order Crossopterygii																																				
Sub-order Osteolepida[16]		×			×	×	×				×		—	—	—			×			×	×				×		×	×		×			×		
Sub-order Cladistia		×		×				×			×		—	—	—	×					×	×				×			×		×			×		
Order Chondrostei	×	×		×	×		×	×		×	×		—	—	—	×	×	×	—	—	—		×		×			×					×	×		
Order Holostei		×	×	×	×	×	×	×		×	×		×			×	×	×		×		×					×		×			×	×	×		
Order Teleostei																																				
Sub-order Malacopterygii	×	×		×	×	×	×	×		×	×	×	×			×	×	×		×		×	×	×	×	×			×		×	×	×	×		
Sub-order Ostariophysi	×	×	×	×	×	×	×	×	×	×	×	×	×			×	×	×		×		×	×		×	×	×		×		×	×	×	×	×	
Sub-order Synbranchii[17]	×			×				×				×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		×		×					×

Sub-order Apodes[17]	X			X				X				X	X			X				X			X				X		X		X				X	X
Sub-order Haplomi		X			X		X	X		X	X		—	—	—		X		X	X		X	X				X		X			X	X	X		
Sub-order Heteromi	X			X			X					X	X			X				X			X				X		X		X			X		
Sub-order Catosteomi	X	X		X	X	X	X	X		X	X		X	X		X	X		X	X		X	X			X	X		X		X	X	X	X	X	X
Sub-order Percesoces	X	X	X	X	X	X	X	X		X	X	X	X			X	X		X	X	X	X	X	X	X	X	X		X	X		X	X	X		
Sub-order Anacanthini		X		X	X		X	X				X	X			X	X			X	X		X			X			X		X	X	X	X		
Sub-order Acanthopterygii																																				
Division Perciformes	X	X		X	X	X				X	X		X			X	X	X	X	X	X	X	X	X		X	X		X		X	X	X	X		
Division Scombriformes	X	X		X	X	X	X	X		X	X	X	X			X	X	X		X	X		X	X	X	X			X		X	X	X	X		
Division Zeorhombi[18]	X	X			X	X	X					X	X			X				X	X		X	X		X			X		X	X		X		
Division Kurtiformes		X			X		X				X		X			X				X			X			X			X				X	X		
Division Gobiiformes	X	X		X	X		X	X	X		X	X	—	—	—		X		X	X	X	X	X			X	X		X		X	X		X	X	
Division Discocephali	X	X		X	X			X				X	—	—	—		X			X	X		X		X	X			X			X		X		
Division Scleroparei		X			X			X			X		—	—	—		X			X	X	X	X		X	X	X		X			X	X	X		
Division Jugulares	X	X		X	X			X	X		X	X	X			X	X			X	X	X	X			X	X		X		X	X	X	X	X	
Division Taeniosomi[19]	X			X			X					X	X			X				X			X			X			X		X			X		
Division Atelaxia[19]	X			X			X					X	X			X				X			X			X			X		X			X		
Sub-order Opisthomi	X			X			X					X	X			X				X		X				X			X		X			X		
Sub-order Pediculati		X	X		X	X		X	X		X		—	—	—		X			X			X				X		X			X			X	X
Sub-order Plectognathi																																				
Division Sclerodermi			X		X	X	X			X			X	X	X	X	X		X	X	X	X	X				X		X			X			X	
Division Gymnodontes			X		X	X	X	X	X	X				X	X		X	X	X	X	X	X	X				X		X			X			X	X
Sub-class Dipneusti	X	X		X	X		X	X			X	X	X			X				X			X	X			X	X	X			X		X		
Fossil forms of uncertain affinities																																				
Palaeospondylidae	X			X				X				X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		X			X		—	—	—
Ostracodermi																																				
Order Heterostraci		X	X		X	X		X	X	X	X		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X			X		X	—	—	—
Order Osteostraci		X			X				X		X		—	—	—		X		—	—	—	X			X			X				X		—	—	—
Order Anaspida[15]		X			X		X				X		—	—	—		X		—	—	—		X		X					X			X			X
Antiarchi			X			X		X			X		—	—	—		X				X		X			X		X			X		X	—	—	—
Arthrodira		X			X			X			X		—	—	—		X		—	—	—	—	—	—	—	—	—	X				X		—	—	—

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[14] This term includes the longitudinal pectorals of the Batoidei. In other groups the dorsal and anal only.

[15] Gill orifices multiple.

[16] Certain members of this order have distinctly trilobed tails which are isobatic.

[17] Gill orifices united ventrally, median.

[18] Some members of this group are rotated through 90°—the Pleuronectidae.

[19] The action of the tails of these fishes if ever used in a locomotor sense is doubtless somewhat epibatic on account of their upturned nature.

TABLE VII

Classification	Body												Longitudinal Structures[14]						Pectoral									Caudal						Gill Orifice		
	Flexures			Form			Section			Flexibility			Flexures			Form			Flexures			Form			Flexibility			Type			Shape					
	Anguilliform	Carangiform	Ostraciiform	Elongate	Fusiform	Truncate	Compressed	Cylindrical	Depressed	Stiff	Intermediate	Flexible	Anguilliform	Intermediate	Ostraciiform	Long and low	Intermediate	Short and high	Anguilliform	Intermediate	Ostraciiform	Broad	Intermediate	Narrow	Stiff	Intermediate	Flexible	Epibatic	Isobatic	Hypobatic	Acuminate	Truncate	Bifurcate	Slit	Oval	Circular
Class Cyclostomata[15]																																				
Order Myxinoides	X			X				X				X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		X		X					X
Order Petromyzontes	X			X				X				X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		X		X					X
Class Pisces																																				
Sub-class Elasmobranchii[15]																																				
Order Pleuropterygii		X			X			X				X	—	—	—		X		—	—	—		X		X			X				X		X		
Order Ichthyotomi		X			X			X				X	X			X					X	X					X		X		X			X		
Order Acanthodei		X		X	X			X			X		—	—	—		X		—	—	—		X		X			X					X	X		
Order Plagiostomi																																				
Sub-order Selachii	X	X		X	X		X	X	X		X	X	—	—	—		X		—	—	—		X		X			X					X	X		
Sub-order Batoidei		X			X	X		X	X		X	X	X				X		—	—	—	—	—	—	—	—	—	X			X	X	X	X		
Order Holocephali	X	X		X	X		X					X				X			X	X	X	X					X	X	X		X		X	X		
Sub-class Teleostomi																																				
Order Crossopterygii																																				
Sub-order Osteolepida[16]		X			X	X	X				X		—	—	—			X			X	X				X		X	X		X			X		
Sub-order Cladistia		X		X				X			X		—	—	—	X					X	X				X			X		X			X		
Order Chondrostei	X	X		X	X		X	X		X	X		—	—	—	X	X	X	—	—	—		X		X			X					X	X		
Order Holostei		X	X	X	X	X	X	X		X	X		X			X	X	X		X		X					X		X			X	X	X		
Order Teleostei																																				
Sub-order Malacopterygii	X	X		X	X	X	X	X		X	X	X	X			X	X	X		X		X	X	X	X	X			X		X	X	X	X		
Sub-order Ostariophysi	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X		X		X	X		X	X	X		X		X	X	X	X	X	
Sub-order Synbranchii[17]	X			X				X				X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		X		X					X
Sub-order Apodes	X			X				X				X	X			X				X			X				X		X		X				X	X
Sub-order Haplomi		X			X		X	X		X	X		—	—	—		X		X	X		X	X				X		X			X	X	X		
Sub-order Heteromi	X			X			X					X	X			X				X			X				X		X		X			X		
Sub-order Catosteomi	X	X		X	X	X	X	X		X	X		X	X		X	X		X	X		X	X			X	X		X	X	X	X	X	X	X	X
Sub-order Percesoces	X	X	X	X	X	X	X	X		X	X	X	X			X	X		X	X	X	X	X	X	X	X	X		X	X		X	X	X		
Sub-order Anacanthini		X		X	X		X	X				X	X			X	X			X	X		X			X			X		X	X	X	X		
Sub-order Acanthopterygii																																				
Division Perciformes	X	X		X	X	X				X	X		X			X	X	X	X	X	X	X	X	X		X	X		X		X	X	X	X		
Division Scombriformes	X	X		X	X	X	X	X		X	X	X	X			X	X	X		X	X		X	X	X	X			X		X	X	X	X		
Division Zeorhombi[18]	X	X			X	X	X					X	X			X				X	X		X	X		X			X		X	X		X		
Division Kurtiformes		X			X		X				X		X			X				X			X			X			X				X	X		
Division Gobiiformes	X	X		X	X		X	X	X		X	X	—	—	—		X		X	X	X	X	X			X	X		X		X	X		X	X	
Division Discocephali	X	X		X	X			X				X	—	—	—		X			X	X		X		X	X			X			X		X		
Division Scleroparei		X			X			X			X		—	—	—		X			X	X	X	X		X	X	X		X			X	X	X		
Division Jugulares	X	X		X	X			X	X		X	X	X			X	X			X	X	X	X			X	X		X		X	X	X	X	X	
Division Taeniosomi[19]	X			X			X					X	X			X				X			X			X			X		X			X		
Division Atelaxia[19]	X			X			X					X	X			X				X			X			X			X		X			X		
Sub-order Opisthomi	X			X			X					X	X			X				X		X				X			X		X			X		
Sub-order Pediculati		X	X		X	X		X	X		X		—	—	—		X			X			X				X		X			X			X	X
Sub-order Plectognathi																																				
Division Sclerodormi			X		X	X	X			X			X	X	X	X	X		X	X	X	X	X				X		X			X			X	
Division Gymnodontes			X		X	X	X	X	X	X				X	X		X	X	X	X	X	X	X				X		X			X			X	X
Sub-class Dipneusti	X	X		X	X		X	X			X	X	X			X				X			X	X			X	X	X			X		X		
Fossil forms of uncertain affinities																																				
Palaeospondylidae	X			X				X				X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		X			X		—	—	—
Ostracodermi																																				
Order Heterostraci		X	X		X	X		X	X	X	X		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X			X		X	—	—	—
Order Osteostraci		X			X				X		X		—	—	—		X		—	—	—	X			X			X				X		—	—	—
Order Anaspida[18]		X			X		X				X		—	—	—		X		—	—	—		X		X					X			X			X
Antiarchi			X			X		X		X			—	—	—		X				X		X			X		X			X		X	—	—	—
Arthrodira		X			X			X			X		—	—	—		X		—	—	—	—	—	—	—	—	—	X				X		—	—	—

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[14] This term includes the longitudinal pectorals of the Batoidei. In other groups the dorsal and anal only.

[15] Gill orifices multiple.

[16] Certain members of this order have distinctly trilobed tails which are isobatic.

[17] Gill orifices united ventrally, median.

[18] Some members of this group are rotated through 90°—the Pleuronectidae.

[19] The action of the tails of these fishes if ever used in a locomotor sense is doubtless somewhat epibatic on account of their upturned nature.

and a considerable part must rest on the judgment of the compiler. In cases where definite information or first hand knowledge was not available the positions of the check marks are based on a study of the extensive literature on fish locomotion, inferences from anatomical data, et cetera. The data concerning fossil forms is based on similarities with existing fishes as noted under "Locomotion of fossil fishes."

The maneuvering abilities of fishes are accomplished, in the main, by differential actions of the locomotor apparatus combined with the presenting of planes to the water when in motion. There are therefore few external structures devoted solely to maneuvering in fishes. On the other hand, the organs concerned with locomotion other than swimming are generally of some definite and highly specialized development. The fins primitively were broad based and relatively fixed in position, (Gregory, 1914) and later took on distinct movements with the necessary accompaniment of a comparatively restricted base.

The habits of fishes are naturally closely connected with their locomotion. Just which is the cause and which the effect is impossible to say in most cases. This connection is especially evident in the movements of fishes other than true swimming, such as burrowing and leaping, for here, as above noted, there are generally limited and peculiar structures to guide one to a correct inference as to their function.

The simple metameral contractions are probably the original primitive vertebrate progressional efforts. They are clearly intimately associated with the reasons for and the functions of the primeval vertebral column.

The following definitions of new terms and the summary bring together in brief form the chief factors entering into the present discussion of fish locomotion and point to the significance of them.

DEFINITIONS OF NEW TERMS.

It has been found necessary and desirable to coin some new terms for the present purposes. The more important types of muscular propulsion and certain body zones have been so designated, using in the former the names of characteristic and well known forms as the word stems, and in the latter definitive terms. It should be noted that the terms ending in "form" refer to types of movement and not to body forms and are therefore not parallel to others such as disciform, fusiform and more recently sagittiform (Schlesinger 1909) which are used to describe the body shapes indicated by the first part of the word. In the present series that part refers to the name of a family exemplifying the characteristic. These may be defined as follows.

Movements of the Body.

Anguilliform Movement.[20] That form of locomotion exemplified by the Anguillidae (*Anguilla*). It consists of a series of sine waves (as in the waving of a flag) which are passed caudad by successive contractions and relaxations of the metameral body muscles. More than one-half a sine curve is formed at least. The pivot is at the base of the skull. See pages 167–169, and Table I.

Carangiform. That form of locomotion exemplified by the typical Carangidae (*Caranx*). It consists of not more than one-half of a sine wave, which is passed caudad by successive contractions and relaxations of the metameral body muscles. The pivot at the beginning of a stroke is at the base of the skull, but moves caudad terminating with the end of the stroke in the peduncle. See pages 175–177, and Table I.

Ostraciiform. That form of locomotion exemplified by the Ostraciidae (*Lactophrys*). It consists of hardly any curve forming at all, the few peduncular myomeres acting almost as a unit in sweeping the flexible tail from side to side. The pivot is in the caudal peduncle. See pages 169–175, and Table I.

Movements of the Longitudinal Structures.

Amiiform. That form of localized anguilliform undulation found in the dorsal fin of the Amiidae (*Amiatus*). See pages 186–190.

Gymnotiform. That form of localized anguilliform undulation found in the anal fin of the Gymnotidae (*Gymnotus*). See page 187.

Balistiform. That form of localized anguilliform and intermediate[21] undulation found in the dorsal and anal of the Balistidae (*Balistes*). The angular divergence of the two fins from the horizontal is complementary, reducing the reactance to a horizontal resultant. See page 187.

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[20] This movement should not be confused with that of serpents (serpentine) moving over solid ground as there are numerous differences which, however, need not be gone into here.

[21] "Carangiform" is not used here for reasons explained on pages 189–190.

Rajiform. That form of localized anguilliform or intermediate undulation found in the expanded lateral pectorals of the Rajidæ (*Raja*). See page 187.

Tetraodontiform. That form of localized ostraciiform undulation found in the dorsal and anal of the Tetraodontidae (*Lagocephalus*). See page 187.

Movements of the Pectorals.

Labriform. That form of localized ostraciiform motion found in the pectorals of the Labridae (*Tautoga*). See page 190.

Diodontiform. That form of localized anguilliform undulation found in the pectorals of the Diodontidae (*Diodon*). See page 190.

Body Sections.

Orthokinetic Part.[22] That portion of a fish's body which moves forward in a rectilinear path through the center of which passes the axis of progression. See page 181.

Cephalic Amphikinetic Part.[22] That anterior portion of a fish's body which does not move forward in a rectilinear path, but oscillates to either side of the orthokinetic part. See page 181.

Caudal Amphikinetic Part.[22] That posterior portion of a fish's body which does not move forward in a rectilinear path, but oscillates to either side of the orthokinetic part. See page 181.

SUMMARY.

(1) The locomotion of fishes has received the attention of students for a long time but there are still many unexplained factors.

(2) The methods basically used by fishes in effecting locomotion are extremely ancient in a geological sense.

(3) The aquatic habitat is of great potency in producing a direct response to streamline requirements, both as regards form and propelling mechanism.

(4) The locomotion of fishes is distinct from that of the tetrapods and shows a certain similarity throughout its various modifications in that the emphasis is placed on the lateral muscles instead of on the paired limbs.

(5) The primary locomotor apparatus of fishes centered in the lateral muscles to induce propulsive contortions in the body itself, has clearly conditioned the origin of the vertebral column.

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[22] The etymology of this term has been suggested by Dr. W. K. Gregory.

(6) The length and degree of flexibility of fishes using such methods determines the form which these movements attain.

(7) A series of graduations is obtained from the waving movements of the eel (anguilliform) through the typical movements of generalized fishes (carangiform) to the wig-wag of rigidly incased fishes (ostraciiform). Although differing superficially, on account of body form, these movements are fundamentally similar.

(8) The thrust effects of the muscular contortions upon the water are direct and not only significant on account of the terminal position of the caudal fin.

(9). Movements similar to those of the body may be localized in various fins and range through a somewhat similar gamut. When localized in various longitudinal structures, the effect of the thrusts is direct, as in the body flexures, (amiiform, gymnotiform, balistiform, tetraodontiform, rajiform), but when in the caudal or pectorals and rarely the pelvics, forward motion is produced by various modifications of the elements entirely dependent, upon position and mechanical circumstances (labriform, diodontiform).

(10) All the movements of fishes when swimming (except exhalation) are fundamentally of an undulatory muscular nature even though obscured by various specializations, and are induced by the serial action of metameral muscles.

(11) A certain point in a fish's body moves straight forward, about which a certain core of material does likewise (orthokinetic part). Anterior and posterior to this are two oscillating parts (cephalic amphikinetic and caudal amphikinetic parts).

(12) The water exhaled through the gill clefts has an effect useful in driving fishes forward, which varies greatly with different forms, being of considerable importance to some and of little or none to others. It may operate mainly by simple reaction (if the gill clefts are circular) or may partake of the induced streamline effect of Paxton (if the gill clefts are long narrow slits).

(13) In the earliest forms in which either single or multiple gill clefts are traceable, they are in the normal position of modern fishes, a fact which indicates the great antiquity of jet propulsion.

(14) Maneuvering in fishes consists mainly of differential application of locomotor efforts that would otherwise produce forward motion, and the presenting of passive surfaces or planes when in motion. There are few external structures in fishes solely devoted to maneuvering.

(15) Turning is accomplished by a variety of methods including body movements, the use of fins and exhalations.

(16) Rising and falling is controlled both by fin movements and the swim-bladder, if present, which is primarily a hydrostatic organ.

(17) Stops are generally made by a braking action of the pectorals if the organization allows of such.

(18) Fishes which reverse their primary locomotor apparatus in coming to a stop, generally also make a practice of travelling backward, for short distances at least. Fishes that show a carangiform or ostraciiform type of body movement are not able to do this, the pectorals playing a relatively large part.

(19) The exhalant respiratory streams of freely suspended fishes make it necessary for them to neutralize these thrusts by various fin actions in order to maintain a stationary position.

(20) A current may either hinder or help locomotion or a given maneuvering act.

(21) While the propelling and steering mechanism of fishes is intimately connected, there is a general tendency to place the burden of the first on the body muscles and that of the latter on the fins.

(22) Locomotor efforts other than swimming, such as flying, creeping, et cetera, are specialized developments and not the common property of any great number of fishes, and are often accompanied by elaborate apparatus developed for that end.

(23) Leaping may be considered a swimming up through the surface of the water at high speed and flying a continuation of it chiefly by planing,whereas burrowing may be considered at the start as a swimming into the soil after which other muscular contractions continue the progress underground.

(24) The entire external character of fishes , from the most general aspect down to minute details, reflects their locomotor qualifications, and indicates the power of their environment in moulding them.

(25) The habits of fishes both are modified by and modify the locomotor qualifications of any given species, these commonly change in the life of an individual, as different habits are acquired during its development.

(26) A great amount of homodynamic adaptation is found throughout fish life in response to certain constant factors found in the aquatic environment, such as the density, pressure, et cetera.

(27) It is the combination of locomotor characteristics that determines a fish's natatorial powers and not the intrinsic qualities of each alone.

(28) Even in fossil fishes the same fundamental characteristics that are found in recent fishes obtain throughout.

(29) The pectoral fins first appear as guiding planes and to offset the depressing action of the epibatic tails. Later they take on definite locomotor movements demanding greater flexibility.

(30) The external factors involved in the swimming of fishes in a straight forward horizontal path through open still water may be tabulated thus.

(A) Effects of planes of pressure
    (1) Body flexures
        (Anguilliform to Ostraciiform)
    (2) Longitudinal fin flexures
        (Localized Anguilliform to Ostraciiform)
    (3) Paired fin flexures
        (Localized Anguilliform to Ostraciiform)
(B) Effects of jets
    (1) Exhalations
        (Paxton's factor to Nozzle reaction)

This table is designed to include all the efforts of fishes to move directly forward under the conditions mentioned above.

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[23] See especially under the following headings: Adaptations, Adhesive disk, Air bladder, Dermal skeleton, Temperature and number of fin rays, Flying fishes and their flight, Form of fishes, Hearing and the static sense, Integument or skin, Locomotion, Metamerism, Sleep of fishes, Technique and methods, Teratology.

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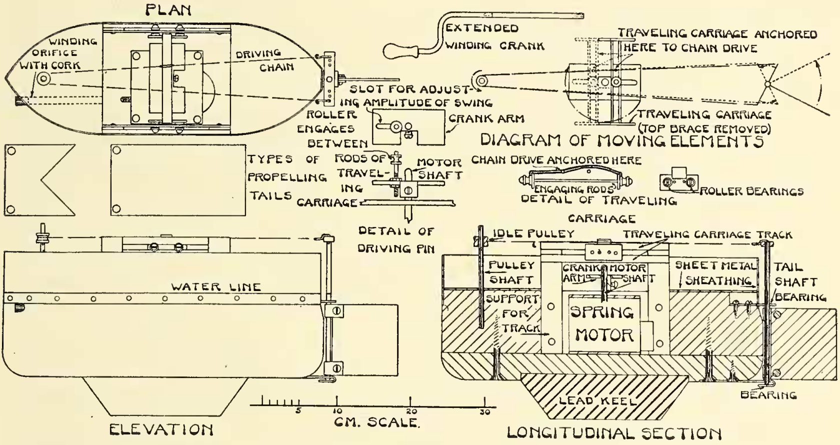

Fig. 80. The ostraciiform model. Working drawing, showing details of construction.

APPENDIX

DESCRIPTIONS OF MECHANICAL DEVICES

The following descriptions and the diagrams accompanying them are herewith appended in order to make more clear the methods used in the phases of the work requiring aids of this nature. They are sufficiently detailed to enable others to construct identical devices if so inclined and allow of a complete check on all such data.

Models.

Two models were constructed in the analysis of the general body movement of fishes. They represent either extreme as discussed under Body Movements.

Ostraciiform Model. The construction of the ostraciiform model (Fig. 40) is shown (Fig 80) and needs scant elaboration in writing. The hull was carved from soft wood and extended upward by a sheathing of sheet metal. The motive power was supplied by a small spring motor, such as is used in phonographs using disc records. No modifications were made on it, the spindle intended to receive the record plate being used as a driving shaft. To this was attached a stiff crank arm supporting a pin bearing a roller. Details of this are shown in the central part of Fig. 80. This grooved roller rested between two

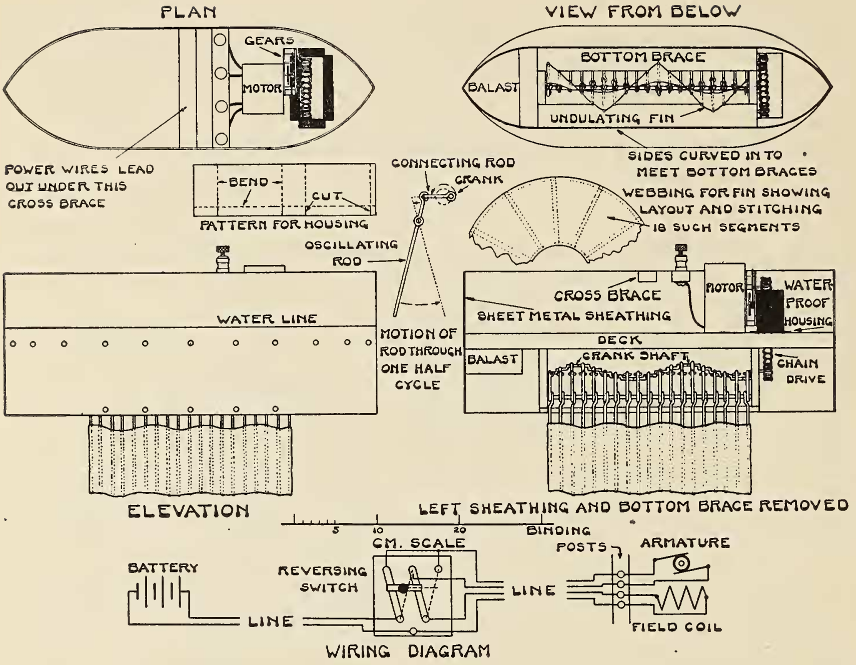

Fig. 81. The anguilliform model. Working drawing, showing details of construction.

parallel rods attached to a travelling carriage to which it imparted a reciprocal motion. A chain attached to either end of the cross arm on the tail piece and passing around a pulley in the bow was secured to one side of the travelling carriage. This imparted a wig-wag motion to the tail piece. The speed of this could be adjusted by regulating the governor on the motor and its amplitude of oscillation could be modified coarsely by slipping the hooks on the ends of the chain in various holes in the tail piece cross arm, as seen in the "Plan" of Fig. 80. Fine adjustment could be obtained by moving the driving pin on the motor shaft in the slot of the crank arm as indicated in the central details. A hole was bored in the hull to accommodate the extended winding crank. A cork prevented any water from being shipped here. Other details of structure are evident on the drawing.

Anguilliform Model. The construction of the anguilliform model (Fig. 49) is illustrated in the working drawing (Fig. 81). The construction of this was somewhat more difficult and as it was desirable to reverse the movements a small electric motor was used for supplying the power. A flat board, the deck, was sheathed above and below with sheet metal, as indicated. A chain of clock work gears was attached to the motor for reducing the speed, the last shaft which supported a sprocket wheel connected with a chain to a similar one at the end of a crank shaft running nearly the full length of the craft. This chain ran through a hole in the deck around which was built a water-tight housing extending above the water line to prevent water reaching the deck and motor. Each crank of the crank shaft was advanced 36° beyond the last, so that every tenth one was in an identical position. To each of these was attached a small connecting rod, linking them with long stiff rods pivoted on another and parallel shaft. Rotation of the crank shaft imparted a wig-wag motion to each of these rods as indicated in the central details of Fig. 81. On account of the placing of the cranks each such rod followed its leader in wig-wagging. Considering them as a whole, a wave was thus caused to pass down them. A piece of thin cloth, doubled, with spacing stitched for the reception of each rod completed the analogy to a longitudinal fin. Power applied by the motor would cause movement of the craft in a direction opposite to the travel of the wave along the series of webbed rods, this being closely analogous to the anal of a gymnotid. Long, flexible insulated wires allowed of freedom of motion. A complete reversal of direction could be obtained by changing the direction of rotation of the motor. This was accomplished by operating a double-poled reversing switch held in the hand and wired as shown in the wiring diagram. Other structural details are evident on the drawing.

Apparatus Other Than Models.

Three pieces of apparatus found to be generally useful were constructed as follows: Their uses were various and are either specifically mentioned in the text or are inferred at various places throughout the body of the paper.

Balance. A balance for determining the position of the center of gravity of fishes was constructed as follows: To a rigid base a vertical metal plate with a

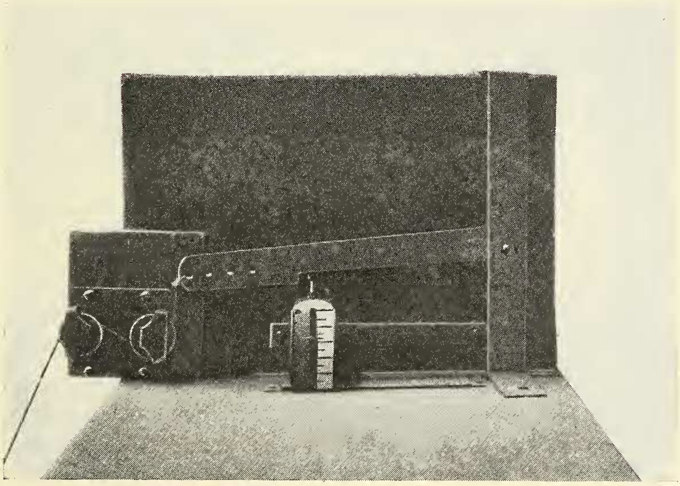

Fig. 82. Dynamometer for determining the tractive pull of fishes.

knife edge was attached. On this was balanced a glass plate to which cross ruled tissue had been glued so that one of the sets of ruling was parallel to the knife edge. Then a fish was laid on the plate with its long axis parallel to the rulings perpendicular to the knife edge by trial until it balanced. Two pins were used as markers fixing the axis through which it balanced. Then the fish was swung through 90° and the process repeated. The intersection of the two lines was over the center of gravity which was half way through the fish (symmetrical from right to left). In this way the data of Fig. 59 was obtained.

Dynamometer. Owing to the fright incident to handling, and the rapid fatigue of fishes the desired data was not obtained by the following described device, but much corollary information was incidentally uncovered. For this reason its description is given. Fig. 82 illustrates it and obviates detailed explanation. A line attached to the long arm and passing over the two pulleys was attached by a bridle to the specimen under experiment. The spring balance then indicated the amount of pull on the line when properly calibrated. This balance could be moved lengthwise of the arm for purposes of leverage depending on the strength of the fish in hand, each position requiring new calibration. However most examples failed to perform in a satisfactory manner, although one *Centropristis* momentarily registered considerably more than its own weight out of water.

Intermittent Light Device. This device aided in the study of fin movements in small fishes. Its external appearance is shown in Fig. 83. A powerful electric lamp burned continuously within the housing and the circular shutter was rotated by a toy electric motor above it. Control was obtained as follows. The length of the periods of light could be varied in relation to the periods of darkness by the adjustable sector in the heavy cardboard shutter attached to the motor shaft by small nuts. The speed of the flashes could be varied to any desired time by a rheostat in the motor circuit. It could be driven at such a speed that the intermittent effect could hardly be detected. As sixteen images per second are about as many as the normal human retina can interpret satisfactorily due to the lag of the sensory nerves, it is clear that a speed of much over 1,000 r.p.m. would be of little value. The device was first tested by rotating a spoked wheel in an otherwise darkened room. By regulating the aperture, and speed it could be made to apparently stand still or rotate in either direction at speeds other than its own. Similar to the effect sometimes seen in motion pictures of wagon wheels. Thus fish fins could often be reduced to apparently slow motion although others, such as the dorsal of *Hippocampus* probably on account of its high speed could not be studied with satisfaction in this way. It seems possible that an accurate measure of its speed might be gotten in some such way by further study.

SUGGESTED LINES OF RESEARCH.

It is particularly patent to the author that the preceding pages are hardly more than a start, and are open to much expansion. Many fascinating digressions from the main theme on subjects which are only touched on here have tempted him considerably in the course of the work and various problems have been noted down. Some of those which seem to promise to be the most prof-

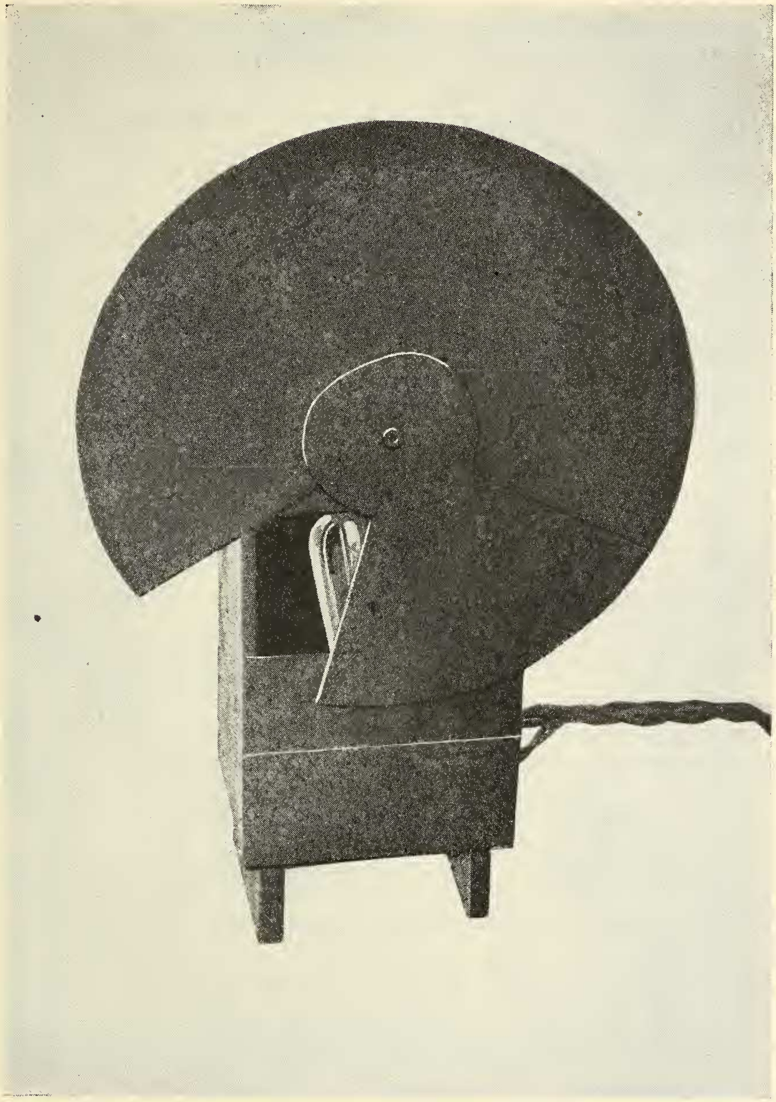

Fig. 83. Intermittent light device for determining the speeds of undulating fins.

itable for future investigation are suggested in the following list. Possibly none of them will be undertaken by the author personally and it is highly desirable that they be investigated by others, if only for the sake of freshness of viewpoint.